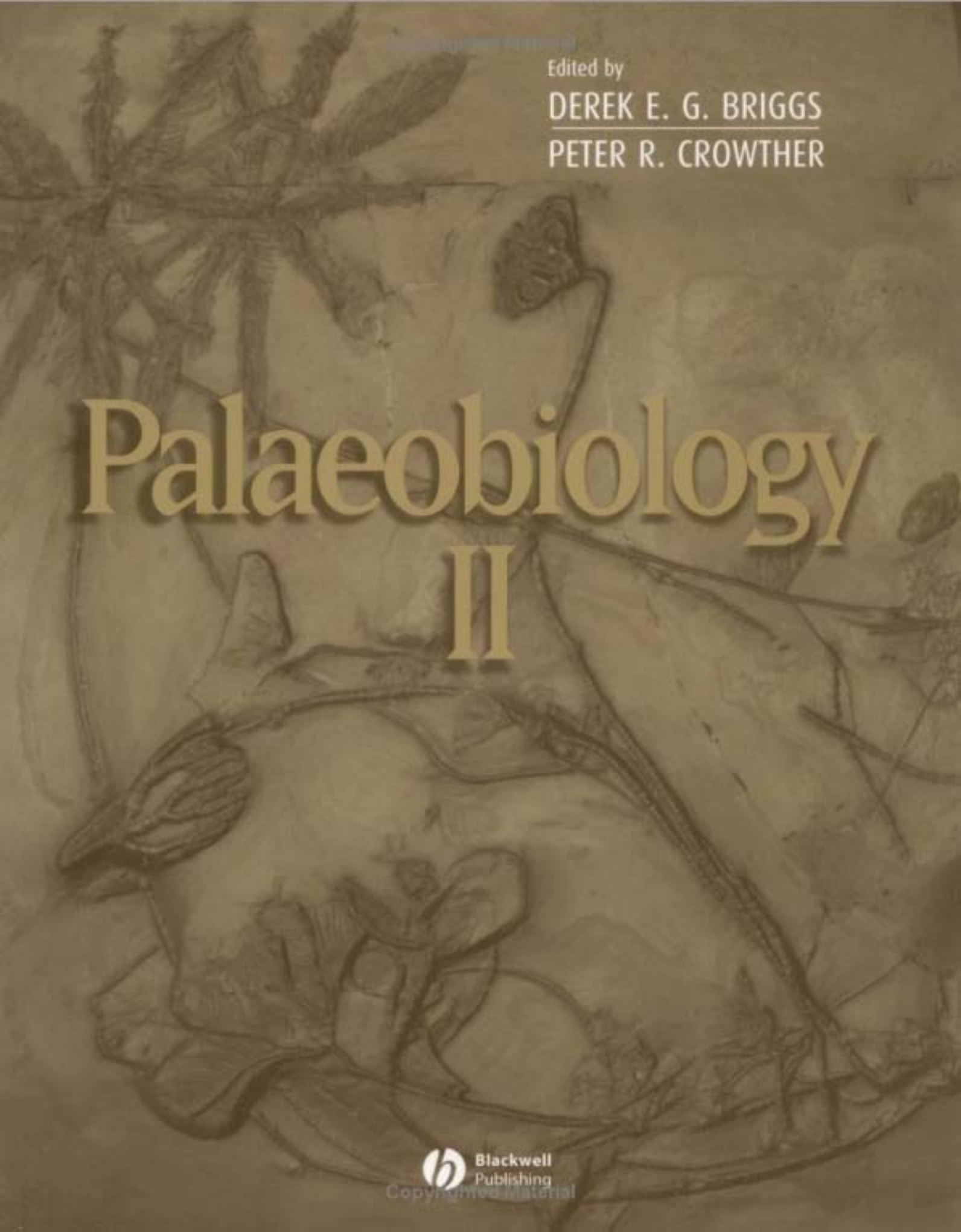

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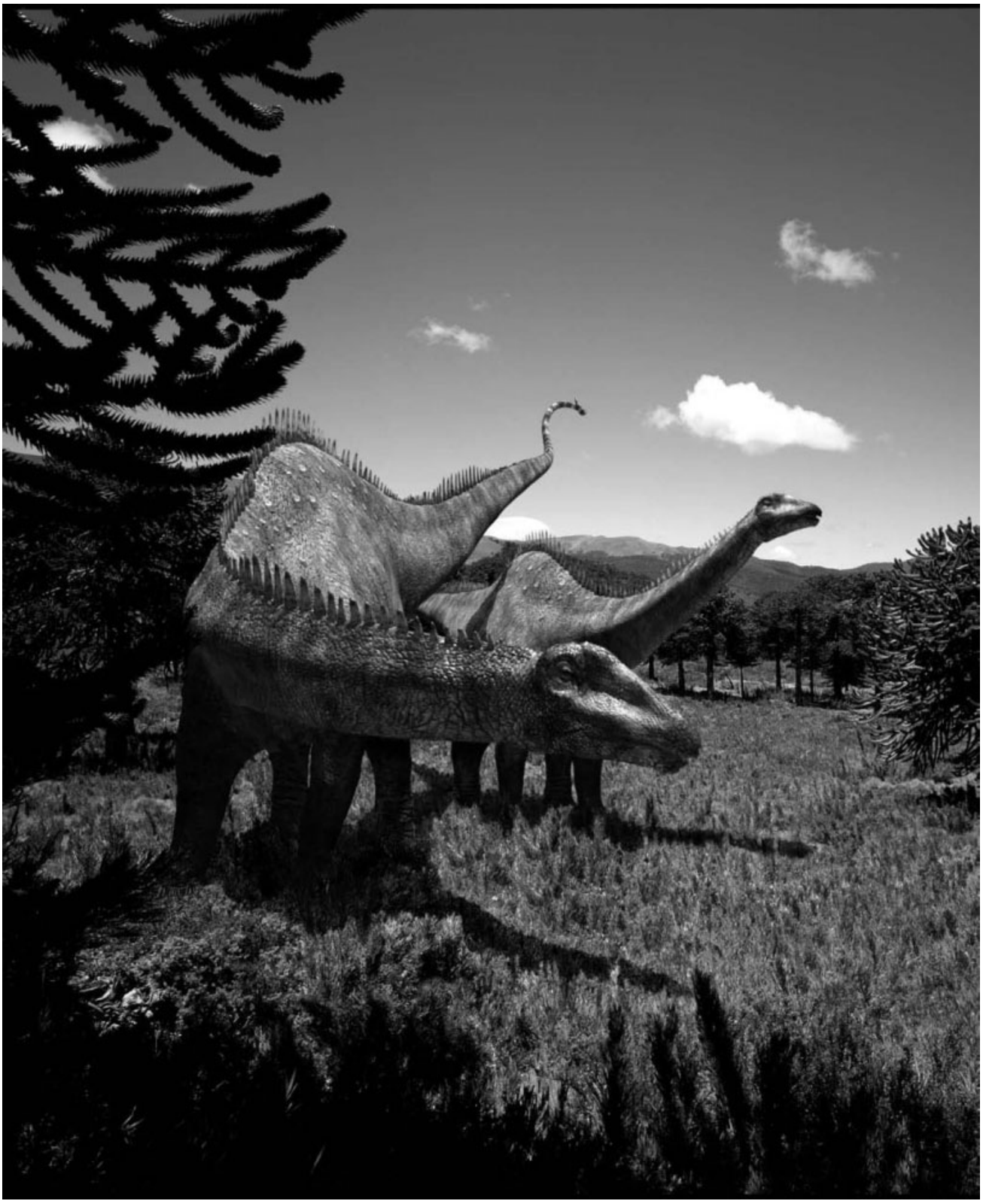

The dinosaur *Diplodocus* as seen in the BBC's acclaimed series 'Walking with Dinosaurs'—the world's first natural history of dinosaurs. © BBC Worldwide Ltd, 1999.

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To the memory of J.J. Sepkoski Jr

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Foreword

EUAN N.K. CLARKSON

President of the
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1998–2000

When *Palaeobiology—a synthesis* appeared in 1990, it was immediately recognized as an invaluable compilation which no palaeobiologist should be without. Each of the articles had been commissioned to provide authoritative and up-to-date information in as concise a form as possible, and only essential references were included. While almost any of these articles could be read by non-experts, their value for advanced students was unquestioned. Where else between two covers could such appropriate and easily mastered source material be found for essays and presentations?

In the decade since the publication of *Palaeobiology—a synthesis*, new data have accumulated, new expertise has arisen, concepts have evolved, and emphases have changed. It is now time for a new synthesis, and here it is—*Palaeobiology II*. Readers familiar with the first book will recognize the main divisions here, but *Palaeobiology II* is by no means a second edition—it is an entirely new book. The great majority of the 137 articles deal with new topics (all are new treatments), and over 100 authors are new. The basic concept that proved so successful in the first book has nevertheless been retained: the articles have been written by recognized authorities in each field; the content is concise but informative; and the accompanying reference lists are brief and up to date.

In all respects this volume is timely, and it will be widely used. The new generation of articles reflects not only the vigorous and exciting developments that are taking place in palaeontology at the opening of the twenty-first century, but also the many links with other scientific disciplines. Palaeontologists today must know about developmental genes and fossil proteins, sequence stratigraphy and fossils, and how to test cladistic analyses against the fossil record. All these topics, and many more, are to be found here. But the scientific themes that have been developed within palaeobiology are also necessary for other sciences, and the book will prove of great value outside its own specific area.

Derek Briggs and Peter Crowther commissioned and edited the articles for *Palaeobiology—a synthesis* and saw the whole gigantic project through to completion. They have again been active; *Palaeobiology II* is a testament to their vision, to the many hours of labour required to realize it, and to the fruitful partnership that they have developed with Blackwell Science.

On behalf of the Palaeontological Association, I wish *Palaeobiology II* the success it deserves. It is very welcome, and the topics covered here cannot fail to interest biologists and palaeontologists of all kinds. Perhaps in another ten years there will be a further version, but this one is unlikely to be quickly superseded.

The
Palaeontological
Association

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MAJOR EVENTS IN THE HISTORY OF LIFE

Cranium of Neandertal (Guattari 1) from Monte Circeo, Italy, approximately two-thirds natural size. (Photograph courtesy of R. Macchiarelli, Museo Nazionale Preistorico Etnografico, Rome.)

1.1 Early Life

1.1.1 Origin of Life

A. LAZCANO

Introduction

'All the organic beings which have ever lived on this Earth', wrote Charles Darwin in *On the Origin of Species by Means of Natural Selection*, 'may be descended from some one primordial form'. It is not known how this first ancestor came into being nor what its nature was. However, the presence of cyanobacteria-like microfossils in the 3.5 billion years old (Ga) Australian Apex sediments (Schopf 1993), deposited only a few million years after the end of the intense bombardment caused by the late accretion of planetesimals left over from the formation of the Solar System, demonstrates that the emergence and early diversification of life on Earth required no more than 500 million years. Together with the inclusions enriched in light isotopic carbon in 3.86 Ga samples from south-west Greenland (Mojzsis *et al.* 1996), these results show that a widespread, complex, and highly diversified Archaean microbiota was thriving soon after the Earth had cooled down and the influx of myriads of comets and asteroids had ceased.

It is unlikely that data on how life originated will be provided by the palaeontological record. There is no geological evidence of the environmental conditions on Earth at the time of the origin of life, nor any fossil register of the evolutionary processes that preceded the appearance of the first cells. Direct information is lacking not only on the composition of the terrestrial atmosphere during the period of the origin of life, but also on the temperature, ocean pH values, and other general and local environmental conditions which may or may not have been important for the emergence of living systems.

The lack of an all-embracing, generally agreed definition of life sometimes gives the impression that what is meant by its origin is defined in somewhat imprecise terms, and that several entirely different questions are often confused. For instance, until a few years ago the origin of the genetic code and of protein synthesis were considered synonymous with the appearance of life itself. This is no longer a dominant point of view; the discovery and development of the catalytic activity of RNA molecules has given considerable support to the idea of an 'RNA world'—a hypothetical stage, before the development of proteins and DNA genomes, during which alternative life forms based on ribozymes existed (Gesteland *et al.* 1999). This has led many to argue that the starting point for the history of life on Earth was the *de novo* emergence of the RNA world from a nucleotide-rich prebiotic soup. Others are more sceptical and believe that it lies in the origin of cryptic and largely unknown pre-RNA worlds. There is even a third group that favours the possibility that life began with the appearance of chemoautotrophic autocatalytic metabolic networks, lacking genetic material.

Despite the seemingly insurmountable obstacles surrounding the understanding of the origin of life (or perhaps because of them), there has been no shortage of discussion about how it took place. Not surprisingly, several alternative and even opposing suggestions have been made regarding how life emerged and what were the defining characteristics of the first organisms. While the classical version of the hypothesis of chemical evolution and primordial heterotrophy needs to be updated, it still provides the most useful framework for addressing the issue of emergence of life.

How can the origin of life be studied?

Of necessity, work on the origin of life should be regarded as enquiring and explanatory rather than definitive and conclusive. This does not imply that our theories and explanations can be dismissed as pure speculation, but rather that the issue should be addressed conjecturally, in an attempt to construct a coherent, non-teleological historical narrative (Kamminga 1991). It is unlikely that the origin of life will ever be described in full detail; at best a sketchy outline, consistent with conditions on the prebiotic Earth (such as its anoxic environment) and the physicochemical properties of the likely molecular precursors of living systems, will be constructed.

The attributes of the first living organisms are unknown. They were probably simpler than any cell now alive, and may have lacked not only protein-based catalysis, but perhaps even the familiar genetic macromolecules, with their ribose-phosphate backbones. It is possible that the only property they shared with extant organisms was the structural complementarity between monomeric subunits of replicative informational polymers, e.g. joining together a growing chain of residues in a sequence directed by preformed polymers. However, such ancestral polymers may not have involved nucleotides. Hence caution must be exercised in extrapo-

lating deep molecular phylogenies back into primordial times. Genome sequencing and analysis is becoming critical for understanding early cellular evolution, but it cannot be applied to events prior to the evolution of protein biosynthesis. Older stages are not yet amenable to this type of analysis, and the organisms at the base of universal phylogenies are cladistically ancient species, not primitive unmodified microbes.

Given the huge gap between the abiotic synthesis of biochemical monomers and the DNA/protein-based last common ancestor of all living systems, it is naive to attempt to describe the origin of life on the basis of available phylogenetic trees. Like a mangrove, the roots of universal evolutionary trees may be submerged in the muddy waters of a prebiotic broth—but how the transition from the non-living to the living took place is still unknown.

Heterotrophic or autotrophic origins of life?

Although the idea of life as an emergent feature of nature has been widespread since the nineteenth century, a major methodological breakthrough by A.I. Oparin and J.B.S. Haldane in the 1920s transformed the origin of life from a purely speculative issue to a workable research programme. This was based on the idea that the first life forms were the outcome of a slow, multistep process that began with the abiotic synthesis of organic compounds and the formation of a 'primitive soup'. There followed the formation of colloidal gel-like systems, from which anaerobic heterotrophs evolved that could take up surrounding organic compounds and use them directly for growth and reproduction.

Many of Oparin's original ideas have been superseded, but his hypothesis provided a conceptual framework for the development of this field. His proposal became widely accepted, not only because it is simpler to envision a heterotrophic organism originating from organic molecules of abiotic origin rather than from an autotroph, but also because laboratory experiments have shown how easy it is to produce a number of biochemical monomers under reducing conditions.

The first successful synthesis of organic compounds under plausible primordial conditions was accomplished by the action of electrical discharges acting for a week over a mixture of CH_4, NH_3, H_2, and H_2O; racemic mixtures of several proteinic amino acids were produced, as well as hydroxy acids, urea, and other organic molecules (Miller 1993). This was followed a few years later by the demonstration of rapid adenine synthesis by the aqueous polymerization of HCN. The potential role of HCN as a precursor in prebiotic chemistry is further supported by the discovery that the hydrolytic products of its polymers include amino acids, purines, and orotic acid (a biosynthetic precursor of uracil). A potential prebiotic route for the synthesis of cytosine in high yields is provided by the reaction of cyanoacetylene with urea, especially when the concentration of the latter is increased by simulating the conditions of an evaporating pond.

The ease with which amino acids, purines, and pyrimidines can form by reactions in a simple vessel strongly suggests that these molecules were components of the prebiotic broth. They would have been associated with many other compounds, such as urea and carboxylic acids, sugars formed by the non-enzymatic condensation of formaldehyde, a wide variety of aliphatic and aromatic hydrocarbons, alcohols, and branched and straight fatty acids, including some which are membrane-forming compounds. The list also includes several highly reactive derivatives of HCN, such as cyanamide (H_2NCN) and its dimer ($H_2NC(NH)NH–CN$), dicyanamide (NC–NH–CN), and cyanogen (NC–CN), which are known to catalyse polymerization reactions. Additional aspects of prebiotic chemistry have been reviewed by Miller (1993), Deamer and Fleischaker (1994), Chyba and McDonald (1995), and Brack (1998).

The synthesis of chemical constituents of contemporary organisms by non-enzymatic processes under laboratory conditions does not necessarily imply that they were either essential for the origin of life or available in the primitive environment. However, the significance of prebiotic simulation experiments is supported by the occurrence of a large array of protein and non-protein amino acids, carboxylic acids, purines, pyrimidines, hydrocarbons, and other molecules in the 4.6 Ga Murchison meteorite (a carbonaceous chondrite which also yields evidence of liquid water) (Miller 1993; Chyba and McDonald 1995). The presence of these compounds in the meteorite makes it plausible, but does not prove, that a similar synthesis took place on the primitive Earth—or is it simply a coincidence?

The evolutionary framework provided by Oparin's theory and methodology has allowed further development and refinement without losing the overall structure and internal coherence of his approach (Kamminga 1991). Several competing approaches to the study of the origin of life coexist today, including proposals for RNA or thioester worlds, for an extraterrestrial origin of the primitive soup's components, and for the role of submarine hot springs as sites for prebiotic chemistry (Chyba and McDonald 1995; de Duve 1995). All, however, are based on the assumption that abiotic organic compounds were a necessary precursor to the appearance of life.

Pyrite formation and the emergence of life

So far, the only serious rival to the heterotrophic theory stems from the work of Wächtershäuser (1988). Accord-

ing to this hypothesis, life began with the appearance of an autocatalytic two-dimensional chemolithotrophic metabolic system based on the formation of the highly insoluble mineral pyrite. Synthesis and polymerization of organic compounds took place on the surface of FeS and FeS_2 in environments that resemble those of deep-sea hydrothermal vents. Replication followed the appearance of non-organismal iron sulphide-based two-dimensional life, in which chemoautotrophic carbon fixation took place by a reductive citric acid cycle, or reverse Krebs cycle, of the type originally described for the photosynthetic green sulphur bacterium *Chlorobium limicola*. Molecular phylogenetic trees show that this mode of carbon fixation and its modifications (such as the reductive acetyl-CoA or the reductive malonyl-CoA pathways) are found in anaerobic archaebacteria and the most deeply divergent eubacteria, which has been interpreted as evidence of its primitive character (Maden 1995). But is the reverse Krebs cycle truly primordial?

The reaction $FeS + H_2S = FeS_2 + H_2$ is a very favourable one. It has an irreversible, highly exergonic (energy liberating) character with a standard free energy change $\Delta G° = -9.23$ kcal/mol, which corresponds to a reduction potential $E° = -620$ mV. Thus, the FeS/H_2S combination is a strong reducing agent, and has been shown to provide an efficient source of electrons for the reduction of organic compounds under mild conditions. Pyrite formation can produce molecular hydrogen, and reduce nitrate to ammonia, acetylene to ethylene, thioacetic acid to acetic acid, as well as more complex synthesis (Maden 1995), including peptide-bonds that result from the activation of amino acids with carbon monoxide and (Ni, Fe)S (Huber and Wächtershäuser 1998). Although pyrite-mediated CO_2 reduction to organic compounds has not been achieved, the fixation under plausible prebiotic conditions of carbon monoxide into activated acetic acid by a mixture of coprecipitated NiS/FeS has been reported (cf. Huber and Wächtershäuser 1998). However, in these experiments the reactions occur in an aqueous environment to which powdered pyrite has been added; they do not form a dense monolayer of ionically bound molecules or take place on the surface of pyrite.

None of the above experiments itself proves that both enzymes and nucleic acids are the evolutionary outcome of surface-bounded metabolism. In fact, the results are also compatible with a more general, modified model of the primitive soup in which pyrite formation is recognized as an important source of electrons for the reduction of organic compounds. It is thus possible that under certain geological conditions the FeS/H_2S combination could have reduced not only CO but also CO_2 released from molten magma in deep-sea vents, leading to biochemical monomers. Peptide synthesis, for instance, could have taken place in an iron and nickel sulphide system (Huber and Wächtershäuser 1998) involving amino acids formed by electrical discharges via a Miller-type synthesis. If the compounds synthesized by this process do not remain bound to the pyrite surface, but drift away into the surrounding aqueous environment, then they would become part of the prebiotic soup, not of a two-dimensional organism. Thus, the experimental results achieved so far with the FeS/H_2S combination are consistent with a heterotrophic origin of life.

The essential question in deciding between these two different theories is not whether pyrite-mediated organic synthesis can occur, but whether direct CO_2 reduction and synthesis of organic compounds can be achieved by a hypothetical two-dimensional living system that lacks genetic information. Proof of Wächtershäuser's hypothesis requires the demonstration of not only the tight coupling of the reactions necessary to drive autocatalytic CO_2 assimilitation via a reductive citric acid cycle, but also the interweaving of a network of homologous cycles which, it is assumed, led to all the anabolic pathways (Maden 1995).

Many original assumptions of the heterotrophic theory have been challenged by our current understanding of genetics, biochemistry, cell biology, and the basic molecular processes of living organisms. The view advocated here assumes that, even if the first living systems were endowed with minimum synthetic abilities, their maintenance and replication depended primarily on prebiotically synthesized organic compounds. An updated heterotrophic hypothesis assumes that the raw material for assembling the first self-maintaining, replicative chemical systems was the outcome of abiotic synthesis, while the energy required to drive the chemical reactions involved in growth and reproduction may have been provided by cyanamide, thioesters, glycine nitrile, or other high energy compounds (de Duve 1995; Lazcano and Miller 1996). This modified version of the classical theory of chemical evolution and primordial heterotrophy can be examined experimentally, and can be expected to generate additional lines of research.

Prebiotic chemistry and the 'primitive soup'

Although it is generally agreed that free oxygen was absent from the primitive Earth, there is no agreement on the composition of the primitive atmosphere; opinions vary from strongly reducing ($CH_4 + N_2$, $NH_3 + H_2O$, or $CO_2 + H_2 + N_2$) to neutral ($CO_2 + N_2 + H_2O$). In general, non-reducing atmospheric models are favoured by atmospheric chemists, while prebiotic chemists lean towards more reducing conditions, under which the abiotic syntheses of amino acids, purines, pyrimidines, and other compounds are very efficient.

The possibility that the primitive atmosphere was

non-reducing does not create insurmountable problems, since the primitive soup could still form. For instance, geological sources of hydrogen, such as pyrite, may have been available; in the presence of ferrous iron, a sulphide ion (SH^-) would have been converted to a disulphide ion (S^{2-}), thereby releasing molecular hydrogen (Maden 1995). It is also possible that the impacts of iron-rich asteroids enhanced the reducing conditions, and that cometary collisions created localized environments favouring organic synthesis. Based on what is known about prebiotic chemistry and meteorite composition, if the primitive Earth was non-reducing, then the organic compounds required must have been brought in by interplanetary dust particles, comets, and meteorites. Recent measurements suggest that a significant percentage of meteoritic amino acids and nucleobases could survive the high temperatures associated with frictional heating during atmospheric entry, and become part of the primitive broth (Glavin and Bada 1999).

This eclectic view, in which the prebiotic soup is formed by contributions from endogenous syntheses, extraterrestrial organic compounds delivered by comets and meteorites, and pyrite-mediated CO reduction, does not contradict the heterotrophic theory. Even if the ultimate source of the organic molecules required for the origin of life turns out to be comets and meteorites, recognition of their extraterrestrial origin is not a rehabilitation of panspermia (the hypothesis that life existed elsewhere in the universe and had been transferred from planet to planet, eventually gaining a foothold on Earth), but an acknowledgement of the role of collisions in shaping the primitive terrestrial environment.

The search for the primordial genetic polymers

There is no evidence of abiotically produced oligopeptides or oligonucleotides in the Murchison meteorite, but condensation reactions clearly took place in the primitive Earth. Synonymous terms like 'primitive soup', 'primordial broth', or 'Darwin's warm little pond' have led in some cases to major misunderstandings, including the simplistic image of a worldwide ocean, rich in self-replicating molecules and accompanied by all sorts of biochemical monomers. The term 'warm little pond', which has long been used for convenience, refers not necessarily to the entire ocean, but to parts of the hydrosphere where the accumulation and interaction of the products of prebiotic synthesis may have taken place. These include not only membrane-bound systems, but also oceanic sediments, intertidal zones, shallow ponds, freshwater lakes, lagoons undergoing wet-and-dry cycles, and eutectic environments (e.g. glacial ponds), where evaporation or other physicochemical mechanisms (such as the adherence of biochemical monomers to active surfaces) could have raised local concentrations and promoted polymerization.

It is difficult to estimate the rate of self-organization of these polymers into replicating systems, because the chemical steps are unknown. Whatever the time scale required for the appearance of an informational polymer, once formed it must have persisted at least long enough to allow its replication. If polymers formed by a slow addition of monomers, this process must have been rapid compared to rates of hydrolysis, especially if a considerable amount of genetic information was contained in the polymer. Self-replicating systems capable of undergoing Darwinian evolution must have emerged in a period shorter than the destruction rates of their components; even if the backbone of primitive genetic polymers was highly stable, the nitrogen bases themselves would decompose over long periods of time. In fact, the accumulation of all components of the primitive soup will be limited by destructive processes, including the pyrolysis of organic compounds in submarine vents. Large amounts of the entire Earth's oceans circulate through the ridge crests every 10 million years, facing temperatures of 350°C or more, and placing an upper limit to the time available for the origin and early diversification of life (Lazcano and Miller 1996).

The popular idea of a hot origin of life is founded largely on the basal position in molecular phylogenies of hyperthermophiles, which exhibit optimal growth temperatures of 80–110°C. Although this hypothesis is also consistent with the emergence of life on a turbulent, hot primitive Earth (which may or may not be true), it is merely an extrapolation of the growth temperature of extant thermophilic prokaryotes. Since most biochemicals decompose rather rapidly at temperatures of 100°C, prebiotic chemistry clearly supports a low-temperature origin of life. A high-temperature origin, under conditions such as those found in deep-sea vents, may be possible, but chemical stability arguments rule out any involvement of the purines, pyrimidines, sugar-phosphate backbone, or even most of the 20 amino acids used by life today: under such extreme conditions, their half-lives are a few seconds. Any theory arguing otherwise must explain not only how life originated under such conditions, but also how the evolutionary transition occurred from the hypothetical high temperature-resistant origin to extant biochemistry.

Bridge(s) to the RNA world

The primitive broth must have been a bewildering organic chemical wonderland in which a wide array of different molecules were constantly synthesized, destroyed, or incorporated into cycles of chemical transformations. Regardless of the complexity of the prebiotic environment, life could not have evolved in the absence

of a genetic replicating mechanism to guarantee the maintenance, stability, and diversification of its basic components under the action of natural selection.

The nature of the system that preceded the ubiquitous DNA-based genetic machinery of extant living systems is unknown, but it must have been endowed with some capacity for self-replication. There is experimental evidence for self-replication in some chemical systems which lack the familiar nucleic acid-like structure. These include replicative micelles and vesicles, and self-complementary molecules which result from the chemical reaction between an amino-adenosine derivative and a complex aromatic ester (cf. Orgel 1992). There are also prions, the infamous infectious agents associated with bovine spongiform encephalopathy (BSE, or 'mad cow disease') and several human neurodegenerative maladies, which may represent a case of phenotypic inheritance that propagate by changing the harmless conformation of a normal protein into an infectious isoform.

Although the above examples suggest that replication may be a widespread phenomenon, these systems do not exhibit heritability, i.e. they are considered autocatalytic but non-informational (Orgel 1992). Hence, they are probably not related to the origin of life. On the other hand, although the properties of RNA molecules make them an extremely attractive model for the origin of life, their existence in the prebiotic environment is unlikely. It is not clear that phosphate esters could have been involved in the first genetic material, and the self-condensation of formaldehyde (i.e. the formose reaction, which appears to be the only plausible route for the prebiotic synthesis of sugars) leads to a complex array of carbohydrates, of which ribose is a minor unstable component. Without phosphate and ribose, RNA molecules could not have formed in the primitive soup. Thus, it is possible that the RNA world itself was the end product of ancient metabolic pathways that evolved in unknown pre-RNA worlds, in which informational macromolecules with different backbones may have been endowed with catalytic activity, i.e. with phenotype and genotype also residing in the same molecules, so that the synthesis of neither protein nor related catalysts is necessary (Lazcano and Miller 1996).

The chemical nature of the first genetic polymers and the catalytic agents that may have formed the pre-RNA worlds are completely unknown and can only be surmised. Modified nucleic acid backbones have been synthesized, which either incorporate a different version of ribose or lack it altogether. Experiments on nucleic acid with hexoses instead of pentoses, and on pyranoses instead of furanose (Eschenmoser 1994), suggest that a wide variety of informational polymers is possible, even when restricted to sugar-phosphate backbones.

One possibility that has not been explored is that the backbone of the original informational macromolecules may have been atactic (e.g. disordered) kerogen-like polymers such as those formed in some prebiotic simulations. There are other possible substitutes for ribose, including open chain, flexible molecules that lack asymmetric carbons. One of the most interesting chemical models for a possible precursor to RNA involves the so-called peptide nucleic acids (PNAs), which have a protein-like backbone of achiral 2-amino-ethyl-glycine, to which nucleic acid bases are attached by an acetic acid (Nielsen 1993). Such molecules form very stable complementary duplexes, both with themselves and with nucleic acids. Although they lack ribose, their functional groups are basically the same as in RNA, so they may also be endowed with catalytic activity.

Although the identification of adenine, guanine, and uracil in the Murchison meteorite supports the idea that these bases were present in the primitive environment (Miller 1993; Chyba and McDonald 1995), it is probable that other heterocycles capable of forming non-standard hydrogen bonding were also available. The Watson–Crick base-pair geometry permits more than the four usual nucleobases, and simpler genetic polymers may not only have lacked the sugar-phosphate backbones, but may also have depended on alternative non-standard hydrogen bonding patterns. The search for experimental models of pre-RNA polymers will be rewarding but difficult; it requires the identification of potentially prebiotic components and the demonstration of their non-enzymatic template-dependent polymerization, as well as coherent descriptions of how they may have catalysed the transition to an RNA world.

Questions for future research

Even though considerable progress has been made in understanding the emergence and early evolution of life, major uncertainties remain. The chemistry of some prebiotic simulations is robust and supported by meteorite analyses, but the gap between these rudimentary experiments and the simplest extant cell is enormous. There is a range of issues relevant to the origin of life, many of which cut across different scientific fields. The geochemical environments under which prebiotic syntheses of biochemical monomers and their polymers could have taken place need to be characterized. Experimental systems to study polymer replication, sequestration of organic compounds, the energy sources that may have been employed by the first replicating systems, and the appearance of metabolic pathways all need to be developed.

The origin of the main features of the genetic code is not understood, but the discovery of the catalytic activity of RNA molecules and the development of novel RNA enzymes through *in vitro* evolution has given

considerable support to the idea that the primitive translation apparatus may have been shaped, at least in part, by interactions between amino acids of prebiotic origin and polyribonucleotides (Gesteland *et al.* 1999). If the current interpretation of the evolutionary significance of these and other properties of RNA molecules is correct, then one of the central issues that origin-of-life research must confront is the understanding of the processes that led from the primitive soup into RNA-based life forms. The search for simple organic replicating polymers will play a central role in this inquiry. Even if the appearance of life remains an elusive issue, redefining the questions that need to be addressed to understand how it took place is, in itself, an encouraging scientific achievement.

References

Brack, A., ed. (1998) *The molecular origins of life*: *assembling pieces of the puzzle.* Cambridge University Press, New York.

Chyba, C.F. and McDonald, G.D. (1995) The origin of life in the Solar System: current issues. *Annual Review of Earth and Planetary Sciences* **23**, 215–249.

Deamer, D.W. and Fleischaker, G.R., eds. (1994) *Origins of life: the central concepts*. Jones and Bartlett, Boston.

de Duve, C. (1995) *Vital dust: life as a cosmic imperative*. Basic Books, New York.

Eschenmoser, A. (1994) Chemistry of potentially prebiological natural products. *Origins of Life and Evolution of the Biosphere* **24**, 389–423.

Gesteland, R.F., Cech, T. and Atkins, J.F., eds. (1999) *The RNA World II*. CSHL Press, Cold Spring Harbor.

Glavin, D.P. and Bada, J.L. (1999) The sublimation and survival of amino acids and nucleobases in the Murchison meteorite during a simulated atmospheric entry heating event. In: *Abstracts of the 12th International Conference on the Origin of Life (11–16 July 1999)*, p. 108. San Diego, California.

Huber, C. and Wächtershäuser, G. (1998) Peptides by activation of amino acids with CO on (Ni, Fe) S surfaces and implications for the origin of life. *Science* **281**, 670–672.

Kamminga, H. (1991) The origin of life on Earth: theory, history, and method. *Uroboros* **1**, 95–110.

Lazcano, A. and Miller, S.L. (1996) The origin and early evolution of life: prebiotic chemistry, the pre-RNA world, and time. *Cell* **85**, 793–798.

Maden, B.E.H. (1995) No soup for starters? Autotrophy and origins of metabolism. *Trends in Biochemical Sciences* **20**, 337–341.

Miller, S.L. (1993) The prebiotic synthesis of organic compounds on the early Earth. In: M.H. Engel and S.A. Macko, eds. *Organic geochemistry*, pp. 625–637. Plenum Press, New York.

Mojzsis, S.J., Arrhenius, G., McKeegan, K.D., Harrison, T.M., Nutman, A.P. and Friend, C.R.L. (1996) Evidence for life before 3,800 million years ago. *Nature* **384**, 55–59.

Nielsen, P.E. (1993) Peptide nucleic acid (PNA): a model structure for the primordial genetic material? *Origins of Life and Evolution of the Biosphere* **23**, 323–327.

Orgel, L.E. (1992) Molecular replication. *Nature* **358**, 203–209.

Schopf, J.W. (1993) Microfossils of the early Archean Apex chert: new evidence of the antiquity of life. *Science* **260**, 640–646.

Wächtershäuser, G. (1988) Before enzymes and templates: theory of surface metabolism. *Microbiological Reviews* **52**, 452–484.

1.1.2 Exploring for a Fossil Record of Extraterrestrial Life

J.D. FARMER

Introduction

While speculation about the possibility of life elsewhere in the Cosmos has been a persistent theme throughout the history of humankind, the last decade of the twentieth century has witnessed a number of important advances in our understanding of the nature and evolution of terrestrial life. These developments have opened up important new possibilities for the existence of living systems elsewhere in the Solar System (or beyond) and have spawned a new interdisciplinary science called 'astrobiology'—the study of the origin, evolution, distribution, and destiny of life in the Cosmos. This new discipline embraces the traditional field of exobiology, which focuses on the origin of life and early biosphere evolution, along with a newer sister discipline, exopalaeontology, which seeks evidence for a fossil record of ancient life or prebiotic chemistry in extraterrestrial materials, or from other planets in the Solar System.

An important legacy of the Apollo space missions was the development of a detailed cratering history for the moon. This led to the view that during early accretion, prior to ≈4.4 Ga, surface conditions on Earth were unfavourable for the origin of life (Chang 1994). As a consequence of frequent giant impacts, magma oceans could have been widespread over the Earth's surface, and volatile compounds, including water and the biogenic elements needed for life's origin, would have been lost to space. Models of early accretion suggest that during the interval 4.4–4.2 Ga impact rates and object sizes declined to a point where the water (and associated organics) delivered to the Earth by volatile-rich impactors (e.g. comets) was retained. A stable atmosphere and oceans probably developed during this time, providing the first suitable environments for prebiotic chemical evolution and the origin of life.

Models also suggest that early biosphere development overlapped with one or more late, giant impacts that were large enough to volatilize the oceans and perhaps sterilize surface environments (Sleep *et al.* 1989). Such events would have frustrated the development of the early biosphere and may have even required that life originate more than once. The most protected habitat during this early period would have been the deep subsurface.

Discoveries of ≈3.45 Ga cellular microfossils from cherts in volcanic sequences in Western Australia (Schopf 1993), and possible 3.86 Ga chemofossils (carbon isotopic signatures) from phosphate-rich metasediments in Greenland (Mojzsis *et al.* 1996) indicate that once the conditions necessary for life's origin were in place, life arose very quickly, perhaps in a few hundred million years or less. This observation significantly improves the possibility that life originated on Mars, or elsewhere in the Solar System where habitable zones of liquid surface water were more ephemeral features of early planetary evolution.

While recent discoveries in Precambrian palaeontology have pushed back the dates for the oldest fossils, molecular phylogenies have also provided important clues about the origin and early evolution of life on Earth, based on the historical record preserved in the genomes of living organisms. Comparisons of genetic sequences in 16S ribosomal RNA indicate that terrestrial life is subdivided into three major domains: the Archaea, the Bacteria, and the Eukarya. It is also apparent that the vast proportion of biodiversity on Earth is microbial. Higher forms of multicellular life appeared quite late in Earth history and make up only a tiny fraction of the total number of species. The deepest branching lineages in the RNA tree are high-temperature forms that utilize reduced inorganic substrates, like sulphur or hydrogen. This suggests that the last common ancestor of life on Earth was a high-temperature ('thermophilic') chemotroph, a view that is consistent with the higher rates of heat flow, volcanism, and frequent impacts that prevailed on the early Earth. However, the RNA tree may reveal little about life's origin (see Section 1.1.1). The thermophilic properties of the most deeply rooted lineages may simply be a legacy of late giant impacts that eliminated all but the highest temperature species.

Possible extant life on Mars and Europa

The discovery of an extensive subsurface biosphere on the Earth opened up exciting new possibilities for the existence of habitable zones elsewhere in the Solar System. On Earth, subsurface habitats harbour many species that are capable of synthesizing organic molecules from simple inorganic substrates. The subsurface is the most compelling environment for extant Martian life because of the possibility that a deep subsurface ground water system may exist at several kilometres depth (Carr 1996). In addition, results from the Galileo mission provide support for the existence of a subsurface ocean beneath the crust of Europa, one of Jupiter's moons. It is postulated that heating of the moon's interior by tidal friction could sustain a subcrustal ocean of liquid water, and sea floor hydrothermal systems (Belton *et al.* 1996). Indeed, the complexly fractured and largely uncratered surface of Europa (Fig. 1.1.2.1) indicates an active ice 'tectonics' involving the periodic upflow of ice-brines from beneath the Europan crust. It is possible that where water welled up from below, it carried life forms or prebiotic chemistry from the underlying ocean and incorporated these materials into surface ices. Terrestrial microbes are known to retain viability at subzero temperatures by exploiting thin films of brine on grain surfaces in permafrost soils. Could viable organisms be present within similar ice-brine environments on Europa? Viability arguments aside, ice could also provide a means for the prolonged cryopreservation of organic materials, accessible to robotic landers.

Exploring for an ancient Martian biosphere

The Viking lander missions showed the present surface environment of Mars to be unfavourable for life due to the absence of liquid water, intense UV radiation, and oxidizing soils. At the same time, images obtained from Mars orbit revealed the early planet to be more Earth-like, with a broad range of surface environments suitable for life. It is likely that habitable environments disappeared from the surface ≈3.8 Ga as Mars began to lose its atmosphere (Farmer and Des Marais 1999). If extant life exists on Mars today, it is likely to be in deep subsurface environments that will be inaccessible to robotic platforms. Deep subsurface drilling will likely require a human presence. However, if life once existed in surface environments, it is likely to have left behind a fossil record in ancient sediments now exposed at the surface. Such deposits could be accessed during the robotic phase of exploration. This simple concept underlies the basic rationale of the present Mars exploration programme.

Studies of the Precambrian fossil record on Earth, and of modern microbial systems that are analogues for those on the early Earth and Mars, provide a conceptual framework for guiding the search for a fossil record on Mars. An understanding of how preservation varies between different groups of microorganisms over extremes of the environment, and how postdepositional, diagenetic changes affect the long-term preservation of microbial biosignatures in rocks, is crucial (Farmer and Des Marais 1999). Such studies allow the formulation of

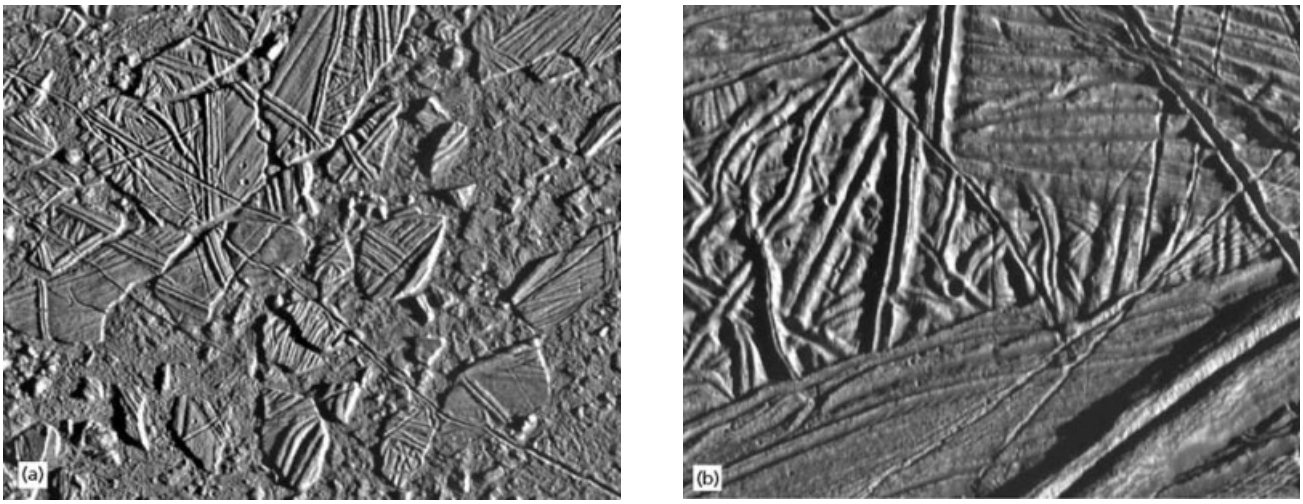


Fig. 1.1.2.1 (a) Galileo orbiter image of the surface of Europa, one of the moons of Jupiter. The surface crust is composed of water ice that has been fractured into irregular blocks. The fracture patterns suggest that the crust was mobilized by a layer of subsurface water which flowed up from below, filling fractures between blocks as they separated. Such observations support the view that Europa once had, and perhaps still has, a subcrustal ocean of liquid water that could sustain life or prebiotic chemistry. The smallest features visible in this image are about 20 m across. (b) Close-up of the surface of Europa showing a complex network of ridged fractures originally formed when plates of ice crust pulled apart. Many ridge segments were later offset along strike–slip faults. The large ridge in the lower right corner of the image is about 1 km across. (Photographs by courtesy of NASA.)

'rules' of preservation that help optimize strategies to explore for past life on Mars and other planetary bodies, such as Europa.

As with Earth-based palaeontology, site selection is crucial for the successful implementation of Mars missions designed to explore for past life. Preservation is a selective process that is strongly dependent upon the biogeological environment. Studies of microbial fossilization reveal that the rapid entombment of microorganisms and their by-products by fine-grained, clay-rich sediments and/or chemical precipitates is of singular importance in enhancing preservation. Favourable geological environments are those where microbial systems coexist with high rates of fine-grained detrital sedimentation, and/or aqueous mineral precipitation. Examples include rapidly mineralizing hydrothermal systems (below the upper temperature limit for life), terminal lake basins (where chemical sediments such as evaporites, fine-grained lacustrine sediments, and sublacustrine cold spring tufas are deposited), and mineralizing soils (e.g. hard-pans, including calcretes, ferracretes, and silcretes). Even if life did not develop on Mars, this exploration strategy is still important because the same sedimentary environments could preserve a record of prebiotic chemistry similar to that which spawned the development of life on Earth. This early prebiotic history has been lost from the terrestrial record.

Mars may preserve the most complete record of early events of planetary evolution anywhere in the Solar System. The 4.56 Ga age of Martian meteorite ALH 84001 (McKay *et al*. 1996) indicates that the ancient, heavily cratered highlands of Mars contain a crustal record extending back to the earliest period of planetary evolution. On Earth, comparably aged crustal sequences have been destroyed by tectonic cycling, metamorphism, weathering, and erosion. In contrast, Mars never developed a plate tectonic cycle and extensive water-mediated weathering and erosion was probably limited to the first billion years or so of the planet's history. Geomorphic features suggest that surface hydrological systems were active until near the end of heavy bombardment (≈3.8 Ga), after which time liquid water quickly disappeared from the surface, presumably as a result of the loss of the Martian atmosphere (Carr 1996).

The preservation of fossil biosignatures is favoured when organisms or their by-products are incorporated into low permeability sedimentary deposits (producing a closed chemical system during diagenesis) of stable mineralogy (promoting a prolonged residence time in the crust). Chemical sediments composed of silica, phosphate, and carbonate, along with fine-grained, clay-rich detrital sediments and water-deposited volcanic ash, are especially favourable lithologies for long-term preservation. This is illustrated by the fact that on Earth most of the Precambrian record is preserved in such lithologies.

Many potential sites for a fossil record have been

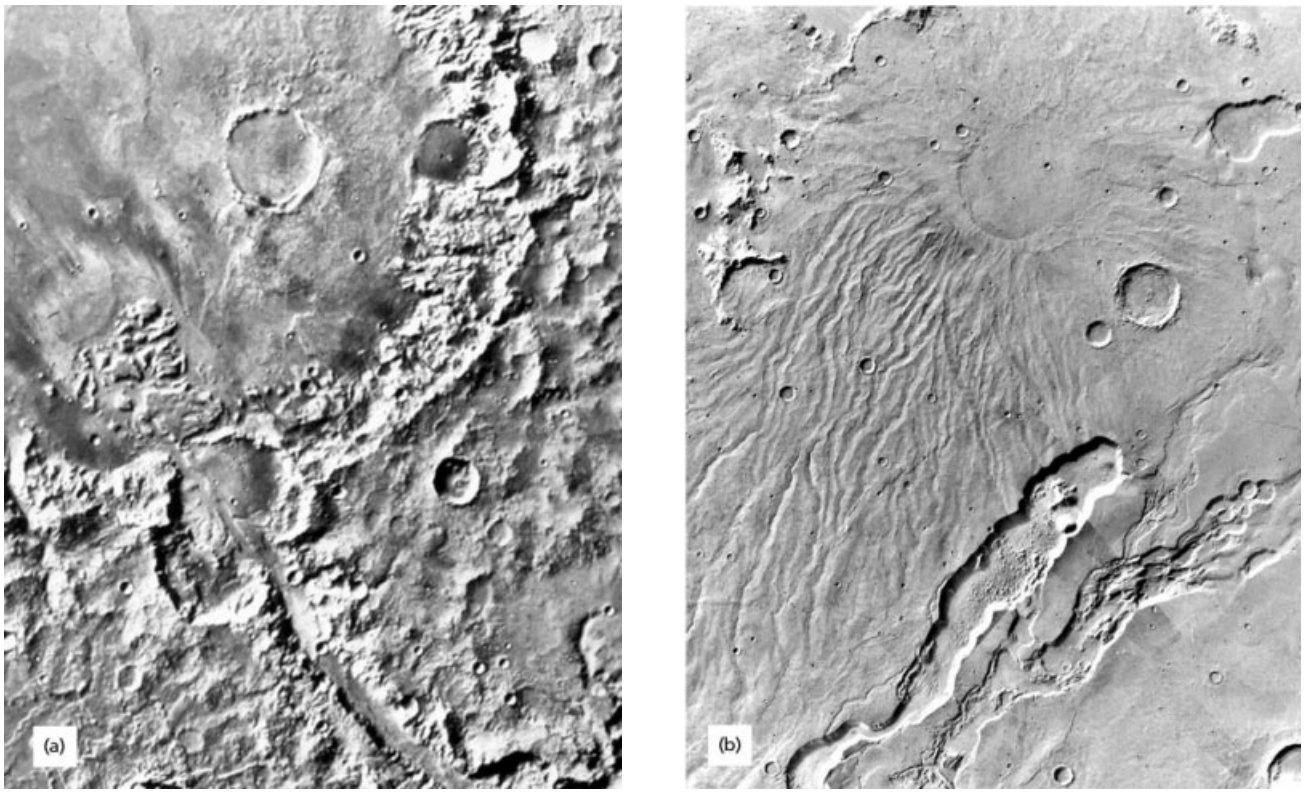


Fig. 1.1.2.2 (a) Gusev Crater, Mars. A large river canyon to the south (Ma'adim Vallis) drained into this ≈150 km diameter crater, depositing a delta where it entered the crater. Geological studies suggest a prolonged hydrological history for this region of Mars, with the Gusev Crater being the site of an ancient palaeolake system. (b) The slopes of Hadriaca Patera, an ancient Martian volcano, show channels radiating downslope, away from the caldera rim (caldera ≈75 km across). These small channels are interpreted to be the result of pyroclastic flows, the channels being subsequently enlarged by sapping flow. The basal slope of Hadriaca Patera was later eroded by outfloods of subsurface water which carved Dao Vallis, a large channel located near the bottom of the photograph (channel ≈45 km wide). The association of subsurface water and a heat source (the subsurface magma that produced the volcano) suggests the potential for sustained hydrothermal activity in this region. (Photographs by courtesy of NASA.)

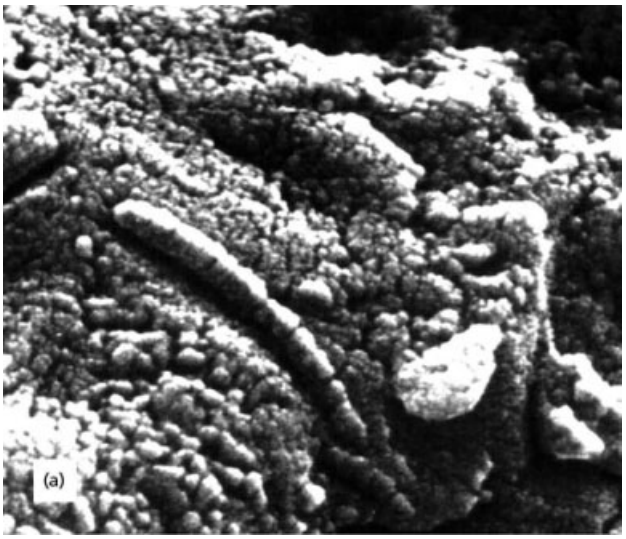
identified on Mars using orbital photographs obtained by Viking (e.g. Fig. 1.1.2.2). However, information about the mineralogical composition of the Martian surface is still lacking. Mineralogy provides important clues about the palaeoenvironment, information needed to determine the best sites for detailed surface exploration. An important exploration goal is to identify aqueous mineral assemblages (of the types that commonly capture and preserve fossil biosignatures) from orbit using spectral mapping methods prior to landed missions. In targeting sites for sample return, evaporative lake basins and hydrothermal sites are given a high priority. In terrestrial settings, the deposits formed in these environments frequently provide optimal conditions for preservation.

Putative signs of life in a Martian meteorite

The report of possible fossil signatures in Martian meteorite Allan Hills 84001 (McKay *et al.* 1996) generated an intense, ongoing debate over the usefulness of a variety of morphological, mineralogical, and geochemical data for detecting biosignatures in ancient rocks. Subsequent work by the broader scientific community indicates that the major lines of evidence used to support the biological hypothesis for ALH 84001 are more easily explained by inorganic processes.

Polycyclic aromatic hydrocarbons (PAHs), such as those found in ALH 84001, are not generally regarded as being diagnostic of life. In addition, it has been shown that a major fraction of the organic matter present in the meteorite exhibits radiocarbon activity, indicating that it originated through terrestrial contamination after reaching the Earth (Jull *et al.* 1998). Although a small fraction of remaining organic matter could be Martian, it has not yet been characterized.

A key test of the biological hypothesis for ALH 84001 is the formation temperature of the carbonates that



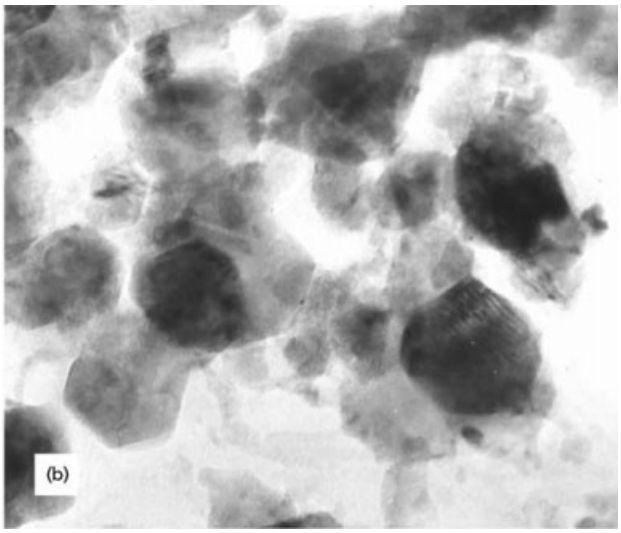


Fig. 1.1.2.3 (a) Scanning electron micrograph of nanostructures found on fracture surfaces of carbonate minerals in Martian meteorite, ALH 84001. The elongated structure in the centre of the image is ≈ 2 μm long and consists of a series of smaller segments each ≈ 0.1 μm wide. (b) Transmission electron micrograph showing small magnetite grains found within carbonate minerals of ALH 84001. The magnetite grains average 15–20 nm wide. Magnetite crystallites in ALH 84001 exhibit epitaxial relationships with the host carbonate grains and screw dislocations suggestive of vapour-phase deposition. (Photographs by courtesy of the Lunar Planetary Institute.)

contain the putative fossil evidence. Carbon and oxygen isotope measurements obtained for carbonates in the Alan Hills meteorite indicate a wide range of formation temperatures, the lowest falling within the range for life (<120°C). Because the carbonates experienced multiple shock events, each with highly localized effects, the spread of isotopic values is perhaps not surprising. However, the lowest temperature estimates are likely to be primary, having been least affected by shock metamorphism (Treiman and Romanek 1998).

Magnetite grains present in the rims of the ALH 84001 carbonates (Fig. 1.1.2.3b) were compared to intracellular magnetite crystals ('magnetosomes') formed by terrestrial magnetotactic bacteria. However, ultrastructural features (spiral defects) discovered in some of the ALH 84001 magnetites suggest that they were formed by vapour deposition at high temperatures. In addition, the ALH 84001 magnetites exhibit epitaxial growth relationships with the host carbonate, and are therefore unlikely to have formed within the cells of bacteria (Bradley *et al.* 1998).

Nanometre-scale morphologies having shapes similar to microbes were observed on some fracture surfaces of carbonates in the ALH 84001 meteorite (Fig. 1.1.2.3a). These were compared to terrestrial 'nanobacteria'. This is an informal term used to describe small (<0.1 μm) rods and spheroids found in rocks which resemble spores or resting stages of microorganisms (see Kirkland *et al.* 1999). At this observational scale, problems often arise in distinguishing biological structures from inorganic forms which originate by self-organizing crystal growth, or as artefacts created during the application of crystalline metal coatings used to prepare samples for scanning electron microscopy (SEM). The putative microfossils in the ALH 84001 meteorite have subsequently been explained by a combination of the above processes. At the nanometre scale, shape is clearly a poor criterion for biogenicity. In the absence of other types of compelling evidence, it is probably best to avoid the use of the term 'nanobacteria', and adopt instead a non-genetic descriptive term, like 'nanostructures', which does not imply an origin.

The apparent refutation of the biological hypothesis for the ALH 84001 meteorite leaves the question of Martian life unresolved. Answering this question is likely to require the careful *in situ* study of Martian samples that formed under aqueous conditions that were favourable for the rapid capture and long-term preservation of biosignatures. Given the difficulty of recognizing ancient microbial signatures in rocks, the return of samples to the Earth for analysis in specialized laboratories may be required for an adequate test of the life hypothesis. The careful re-examination of biological evidence for the ALH 84001 meteorite has improved the basis for interpreting the Precambrian record on Earth by establishing more rigorous standards for biogenicity in ancient materials. The broadly based effort has also helped to prepare the scientific community for a series of Mars sample return missions tentatively scheduled to begin in 2009.

References

Belton, M.J.S. and Galileo SSI Team (1996) Galileo's first images of Jupiter and the Galilean satellites. *Science* **274**, 377–385.

Bradley, J.P., McSween, H.Y. and Harvey, R.P. (1998) Epitaxial growth of nanophase magnetite in Martian meteorite Allan Hills 84001: implications for biogenic mineralization. *Meteoritics Planetary Science* **33**, 765–773.

Carr, M.H. (1996) *Water on Mars*. Oxford University Press, London.

Chang, S. (1994) The planetary setting of prebiotic evolution. In: S. Bengston, ed. *Early life on Earth*, pp. 10–23. Nobel Symposium no. 84. Columbia University Press, New York.

Farmer, J.D. and Des Marais, D.J. (1999) Exploring for a record of ancient Martian life. *Journal of Geophysical Research—Planets* **104** (E11), 26977–26995.

Jull, A.J.T., Courtney, C., Jeffrey, D.A. and Beck, J.W. (1998) Isotopic evidence for a terrestrial source of organic compounds found in Martian meteorites Allan Hills 84001 and Elephant Moraine 79001. *Science* **279**, 366–369.

Kirkland, B.L., Lynch, F.L., Rahnis, M.A., Folk, R.L., Molineux, I.J. and McLean, R.J.C. (1999) Alternative origins for nanobacteria-like objects in calcite. *Geology* **27**, 347–350.

McKay, D.S., Gibson, E.K., Thomas-Keprta, K.L., Vali, H., Romanek, C.S., Clemett, S.J., Chillier, X.D.F., Maechling, C.R. and Zare, R.N. (1996) Search for past life on Mars: possible relic biogenic activity in Martian meteorite ALH 84001. *Science* **273**, 924–930.

Mojzsis, S.J., Arrhenius, G., McKeegan, K.D., Harrison, T.M., Nutman, A.P. and Friend, C.R.L. (1996) Evidence for life on Earth before 3,800 million years ago. *Nature* **384**, 55–59.

Schopf, J.W. (1993) Microfossils of the Early Archean Apex Chert: new evidence of the antiquity of life. *Science* **260**, 640–646.

Sleep, N.H., Zahnle, K.J., Kasting, J.F. and Morowitz, H. (1989) Annihilation of ecosystems by large asteroid impacts on the early Earth. *Nature* **342**, 139–142.

Treiman, A.H. and Romanek, C.S. (1998) Bulk and stable isotopic compositions of carbonate minerals in Martian meteorite Allan Hills 84001: no proof of high formation temperature. *Meteoritics Planetary Science* **33**, 737–742.

1.1.3 Life in the Archaean

R. BUICK

Introduction

When did life on Earth first appear? What were primordial organisms like? How and where did they live? Though these are age-old philosophical and theological questions, they also have scientific significance. Clearly, Earth's history would have been different if abundant, diverse life had arisen when the crust solidified, perhaps 4.5 billion years ago, rather than halfway through geological time, at the end of the Archaean (2.5 Ga).

To answer these questions empirically, palaeontological and geochemical relics of an Archaean biota are required, but finding such evidence can be difficult. Archaean rocks are rare because the exposed rock mass diminishes markedly with age due to erosion, burial, and subduction. Many that remain are poorly preserved because the probability of destructive deformation or metamorphism increases with age. However, in a few ancient cratons, relatively untraumatized Archaean supracrustal rocks still exist in reasonable abundance, permitting palaeobiological investigation of suitable facies. These consist mainly of kerogenous cherts and shales, banded ironstones, and carbonates of various compositions, but more exotic lithologies (sandstones, palaeosols, hydrothermal deposits) can also yield useful data.

As even the most pristine Archaean rocks have complex histories, their sedimentary environment, stratigraphic relationships, postdepositional evolution, and geochronology must be fully understood to ascertain whether any biological remains are indeed ancient and not younger contamination. However, these basic geological data are rarely available in many Archaean terrains. Furthermore, as early organisms were probably small, simple, and subtle in their environmental impact, the biogenicity of putative Archaean fossils is often ambiguous. More studies of modern microbes, their biogeochemical interactions, and their inorganic mimics are needed to resolve this issue. Perhaps most importantly, it is essential to approach Archaean palaeobiology from first principles, because the nature of the early fossil record is unpredictable, and to subject all data to severe scrutiny, because real discoveries are of such significance.

How are relics of Archaean life preserved?

Microfossils

The ideal form of Archaean palaeobiological evidence is the preserved remains of the organisms themselves (see Section 3.4.2). As no macrofossils have ever been found in rocks older than 2.1 Ga, the search for Archaean fossils has been largely conducted by microscopy. The most convincing are barely of Archaean age, ≈2.52 Ga from the Transvaal Supergroup of South Africa (Lanier 1986; Klein *et al.* 1987; Altermann and Schopf 1995). The assemblages (Fig. 1.1.3.1) contain solitary or paired ellipsoids (0.2–2.5 μm), solitary, paired or clustered spheroids (1.5–20 μm), solitary tubular filaments (diameter 0.5–3 μm) and interwoven mats of tubular filaments (diameter 10–30 μm), all composed of kerogen that is isotopically

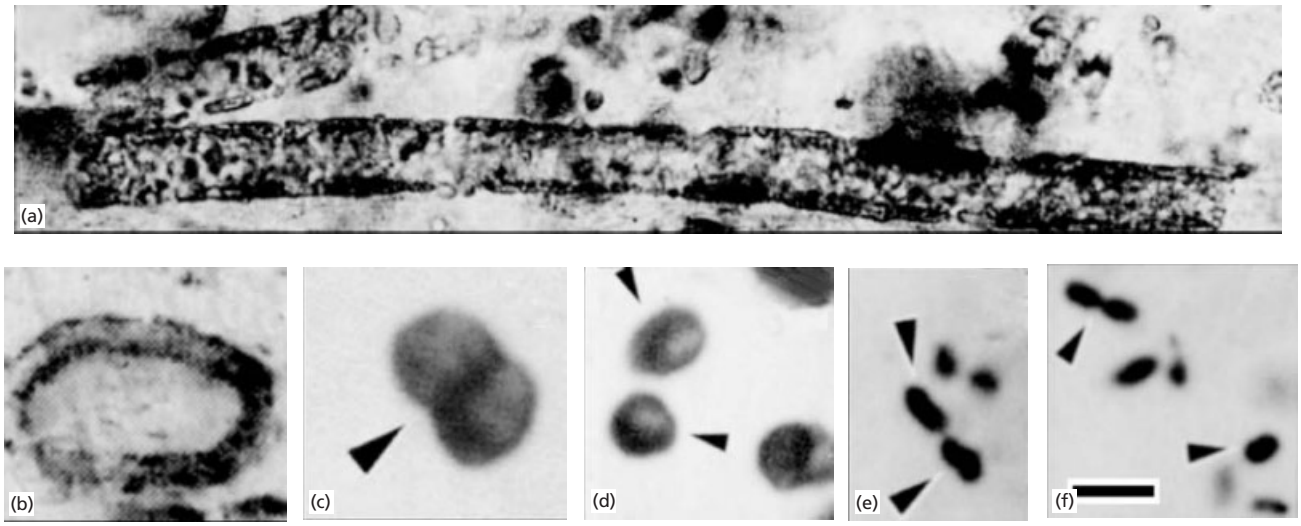


Fig. 1.1.3.1 Archaean microfossils from the 2.52 Ga Transvaal Supergroup, South Africa. (a) Filaments in longitudinal section. (b) Filament in cross-section. (c,d) Spheroids, paired and clustered. (e,f) Ellipsoids, solitary and paired. Bar = 18.7 μm for (a); 6.8 μm for (b); 1.8 μm for (c); 3.0 μm for (d) and (f); 2.5 μm for (e).(a,b, From Klein *et al.* 1987, with permission from Elsevier Science; c–f, from Lanier 1986.)

similar to younger biological carbon. These objects are undoubtedly syngenetic and compellingly biogenic, representing uncontroversial microfossils.

Older assemblages are more problematic. Very rare, poorly preserved, filamentous structures have been reported from the 2.72 Ga Tumbiana Formation of Australia (Schopf and Walter 1983), but it is not clear that these have an organic composition or a matting habit, both common characteristics of biogenic filaments. Numerous simple spheroidal and filamentous objects of carbonaceous composition have been described from the 3.45–3.25 Ga Swaziland Supergroup of South Africa, with perhaps the most lifelike from the Kromberg Formation (Walsh 1992). These hollow cylindrical filaments (diameter 1.5–5 μm) are composed of kerogen much finer in grain size than in the surrounding matrix, making an inorganic origin difficult to envisage. Filaments, some of which are spectacularly lifelike, have also been reported from North Pole, Australia, in the ≈3.46 Ga Warrawoona Group (Awramik *et al.* 1983). These, however, are probably younger contaminants. They are composed of brown kerogen, indicating lesser metamorphism than experienced by indigenous Warrawoona kerogen, which is black (as befits organic matter exposed to temperatures of ≈300°C). The fossiliferous sample was evidently collected on an exhumed unconformity between the early Archaean Warrawoona Group and the late Archaean (≈2.7 Ga) Fortescue Group, suggesting that they could have been emplaced in their host rock during deposition of the latter. Similarly, some of the septate filaments and clustered spheroids reported from cherts in the <3.46 Ga Apex Basalt, Australia (Schopf and Packer 1987), are dark brown—a colour incompatible with the greenschist metamorphic grade of the surrounding rocks. This suggests that these objects are either not organic or not indigenous, making their claimed status as the oldest known microfossils dubious.

Stromatolites

Many assemblages of stromatolites (laminated sedimentary structures accreted as a result of microbial growth, movement, or metabolism) are now known from Archaean rocks (see Section 4.1.2). Those of late Archaean age (<3.0 Ga) are generally regarded as biogenic (Fig. 1.1.3.2). However, the origin of older stromatolite-like structures is controversial. Based on a detailed structural analysis of three of the better-known occurrences, it has been argued that all those older than 3.2 Ga are in fact abiogenic evaporative precipitates, hydrothermal accretions, or deformational features (Lowe 1994). However, this study neglected the most thoroughly described, best illustrated, and most complex stromatolitic occurrence so far reported from the early Archaean, i.e. the bed of stratiform, pseudocolumnar, and semicolumnar structures from the Warrawoona Group (>3.46 Ga) at North Pole, Australia (Buick *et al.* 1981). These defy categorization as evaporative, hydrothermal, or deformational features, as they have

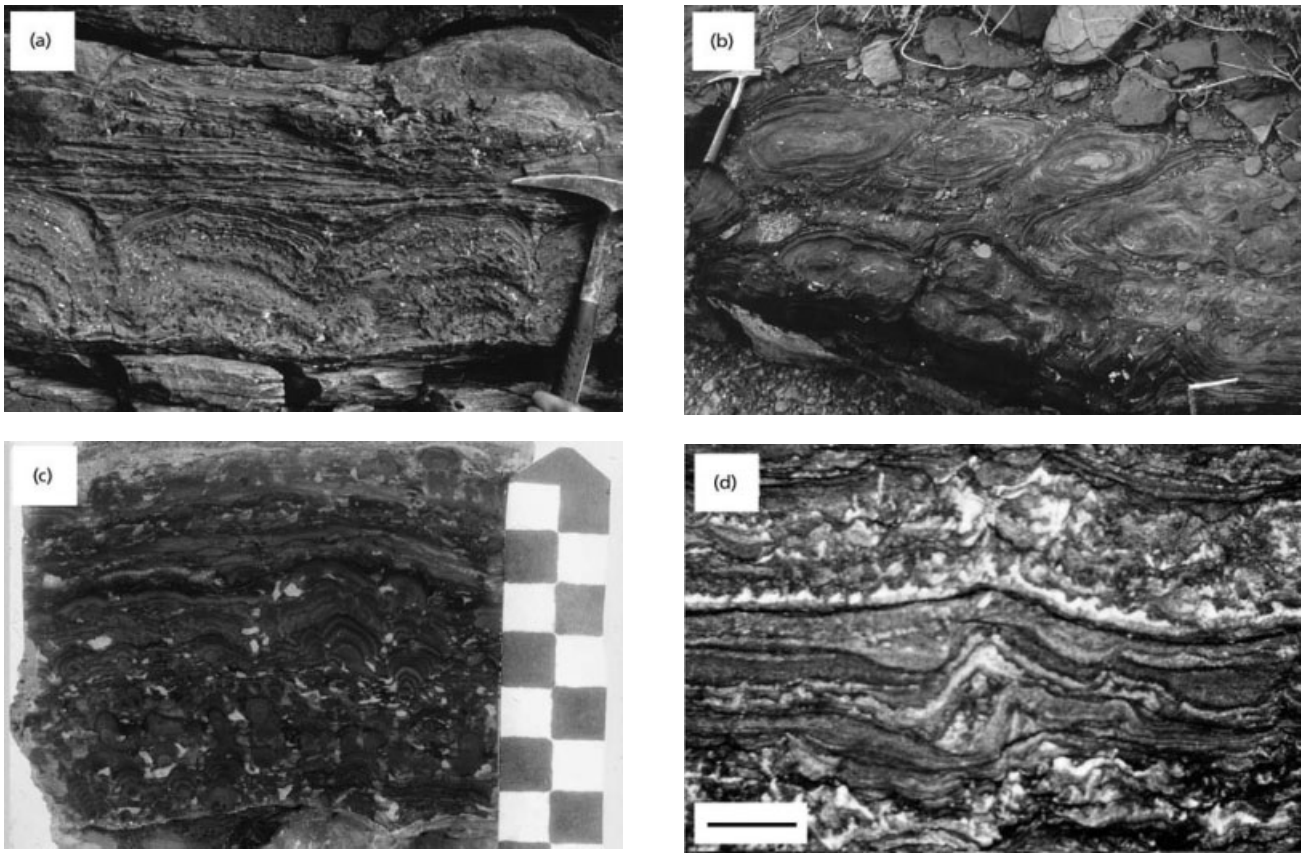


Fig. 1.1.3.2 Stromatolites from the 2.72 Ga Tumbiana Formation, Fortescue Group, Billadunna, Australia. (a) Cross-section of pseudocolumnar structures with fenestrae (white spots). (b) Plan view of domical crests of pseudocolumnar structures. (c) Cross-section slab of pseudocolumnar structures showing a finer order of flexure within the major structures and alternating light and dark laminae with interspersed fenestrae (white patches). (d) Thin-section of wrinkly microlaminae with cuspate palimpsests (white) after tufted clusters of microbial filaments. Scale in (c) is in centimetres. Bar = 3.15 mm for (d).

several orders of lamination contorted into several orders of flexures, only moderate morphological inheritance, and lenses of desiccated fragments filling troughs between flexures (Fig. 1.1.3.3). Moreover, their kerogenous microlaminae, which thicken over flexures, suggest biological inhabitants. So, it is perhaps premature to dismiss all early Archaean stromatolites as abiogenic on the strength of a limited survey.

Mathematical models show that stromatolite-like structures with fractal growth-surface geometry can be produced inorganically by the interaction of sedimentation, precipitation, and gravitation (Grotzinger and Rothman 1996). If so, early in Earth's history when inorganic carbonate evidently precipitated voluminously on the sea floor and in the water column, such structures could have formed in abundance. However, at least some early Archaean stromatolites, including those from North Pole, do not possess self-similar growth surfaces and are quite irregular on several scales, so perhaps they are indeed biogenic. But clearly a biological origin cannot be assumed for such ancient structures without multiple lines of supporting evidence, preferably including microfossils indicating by their disposition or composition an active involvement in sedimentation.

Carbon isotopes

A more continuous record of Archaean biology is preserved in the carbon isotope ratios of sedimentary rocks. As autotrophy incorporates the light stable isotope of carbon (^{12}C) into newly synthesized organic matter in preference to the heavy isotope (^{13}C), any kerogen ultimately derived from autotrophic organisms will have a $\delta^{13}C_{org}$ value fractionated from that of the bulk Earth. Reflecting this biotic accumulation of ^{12}C, carbonate precipitated from water inhabited by autotrophs will be somewhat enriched in ^{13}C. So, on the modern Earth, $\delta^{13}C_{org}$ averages around –25‰ and marine $\delta^{13}C_{carb}$ is generally about 0‰, compared with a mantle value of about –5‰. This fractionation pattern can be traced back through the sedimentary record (Fig. 1.1.3.4b), with a few significant but temporary variations, to the end of

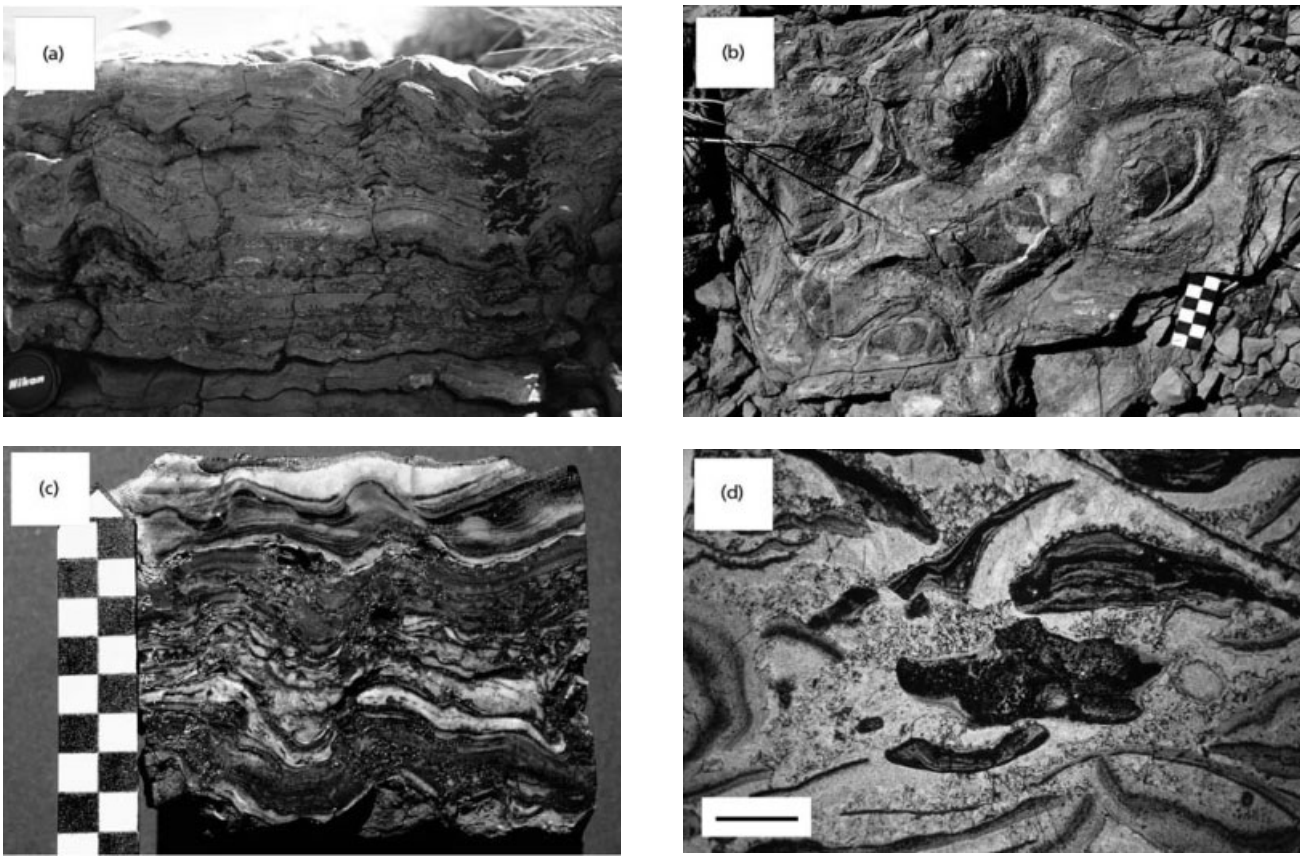


Fig. 1.1.3.3 Stromatolites from the >3.46 Ga Warrawoona Group, North Pole, Australia. (a) Cross-section of pseudocolumnar structures with flexures initiated at, and propagating to, different heights within the bed. (b) Plan view of domical crests to pseudocolumnar structures. (c) Cross-section slab of pseudocolumnar structures showing a finer order of flexure within the major structures and alternating light and dark laminae on several scales. (d) Thin-section of ripped-up curved intraclasts with wrinkly kerogenous microlaminae accumulated in a trough between pseudocolumns. Scale in (b) and (c) is in centimetres. Bar = 0.44 mm for (d).

the Archaean. The only major trend is a gradual increase in the difference between $\delta^{13}C_{org}$ and $\delta^{13}C_{carb}$, from –25‰ to –35‰, through the Proterozoic. When ^{13}C loss by thermal alteration during diagenesis and metamorphism is considered, this trend is enhanced, with corrected $\delta^{13}C_{org}$ values at the Archaean–Proterozoic boundary averaging around –40‰. Such a pattern indicates the persistence of autotrophic fractionation through time, with the trend possibly imposed by progressive growth in the amount of organic carbon buried in sedimentary rock, steadily removing more of the light isotope from biological availability.

The Archaean carbon isotope record is less simple. Back to 3.5 Ga, $\delta^{13}C_{carb}$ values for most low-grade metasedimentary rocks average close to 0‰, suggesting biological autotrophy (Schidlowski 1993). However, carbonates associated with banded ironstones are distinctly light (–3‰ to –10‰), probably due to precipitation from the suboxic depths of a stratified ocean rich in light bicarbonate derived from biological respiration. The only older sedimentary carbonates occur in highly metamorphosed terrains and it is contentious whether they are of sedimentary or metasomatic origin. Thus the isotopic record of carbonate carbon can be interpreted as showing clear evidence for life almost, but not quite, back to the beginning of the geological record. Organic carbon is consistent with such an interpretation. Archaean $\delta^{13}C_{org}$ values are generally about –30‰ which, after correction for metamorphic loss of light hydrocarbons, translates to original ratios nearer –40‰, similar to early Proterozoic values indicative of autotrophy. But before ≈3.5 Ga, the organic record, like its carbonate equivalent, is sparse, metamorphosed, and controversial.

Organic geochemistry

Organic geochemical analysis of Archaean sedimentary rocks was widely used in early attempts to determine the antiquity of life, but is now rather discredited. Most

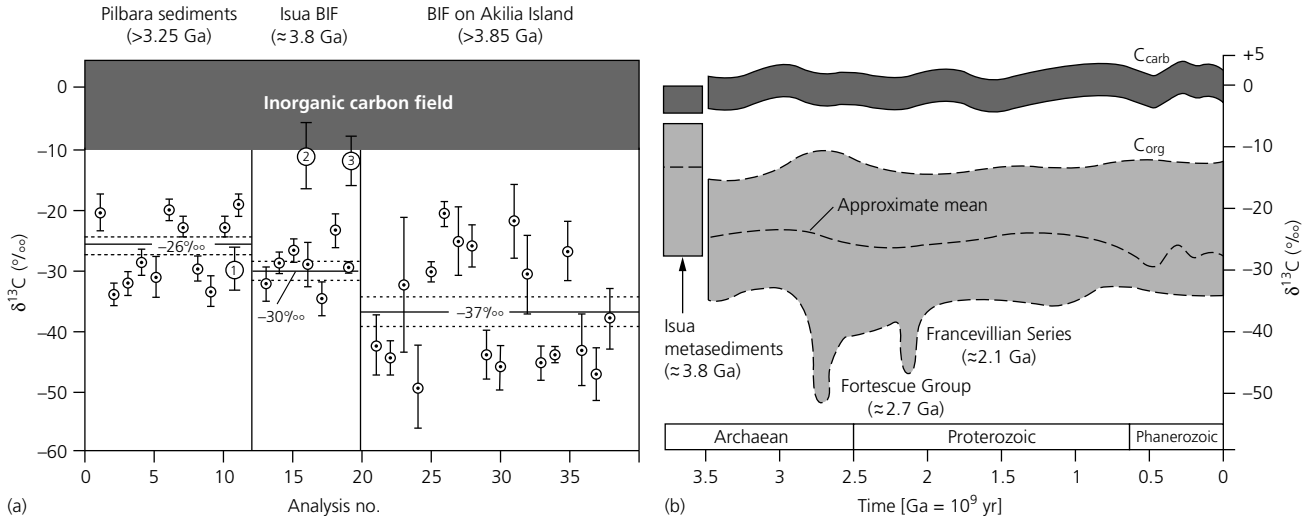


Fig. 1.1.3.4 Sedimentary carbon isotope values through time. (a) Ion-microprobe analyses of minute graphite inclusions within apatite crystals in several early Archaean iron-formations, including the Isua and Akilia, Greenland. Each analysis is marked by a ring with 1σ standard deviations indicated by vertical bars; numbered rings and bars represent whole-rock organic carbon values previously obtained; weighted means of data represented by solid lines with 2σ confidence interval marked by dotted lines; dark bar at top represents range of values for sedimentary carbonate. (b) Range of whole-rock organic carbon and carbonate values from 3.8 to 0 Ga. (a, Reprinted with permission from *Nature* (Mojzsis *et al*. 1996), copyright 1996 Macmillan Magazines Limited; b, from Schidlowski 1993.)

investigations concentrated on solvent extraction, searching for soluble organic compounds derived from distinctive biological molecules ('biomarkers'). These yielded *n*-alkanes, alkanoic acids, isoprenoid alkanes, porphyrins, and amino acids from rocks as old as the ≈3.4 Ga Swaziland Supergroup of southern Africa and even the >3.7 Ga Itsaq Gneiss of Greenland. However, all of these compounds were obtained at concentrations permitted by the permeability of their host rocks, allowing them to have migrated into the rock after deposition, and some of the chiral compounds were still optically active, which if indigeneous should have long since been racemized. Hence, these soluble compounds are now generally regarded as younger contamination (Hayes *et al*. 1983).

In attempts to overcome this problem, Archaean insoluble kerogen has been analysed by pyrolysis. This produced a variety of aliphatic, aromatic, and heterocyclic compounds, once thought to be indigenous degradation products of primordial organisms. However, irreversible contamination of kerogen by younger hydrocarbons can occur to such an extent that, without determination of yield proportions for all products (as in most Archaean studies), pyrolysis is ineffective in the search for early life (Hayes *et al*. 1983).

However, the discovery of Archaean oil and its degradational derivatives (Fig. 1.1.3.5) offers new opportunities for organic geochemical investigation of the early biota (Dutkiewicz *et al*. 1998). If the oil proves to come from biological sources, it should yield chemical fossils of the organisms from which it was derived. Although the known Archaean oil exists in minute quantities, it is sealed in fluid inclusions that have protected it from pollution since its entrapment. So, if modern contamination in the laboratory can be avoided (a difficult but perhaps not insurmountable problem), it may be possible to extract biomarkers that reveal something about the broad biological affinities of the precursor organisms, their metabolic pathways, and their habitat preference.

When did life first appear?

The oldest known rocks that could possibly contain relics of life are >3.7 Ga metasediments (upper amphibolite facies: >650°C with multiple deformations) in the Itsaq Gneiss Complex of Greenland. From these, many microfossils and biomarkers have been reported but all have been subsequently discounted. Evidently, at such high metamorphic grades, only isotopic geochemistry can provide satisfactory evidence of life, but even then its interpretation is not straightforward. Carbon isotope values are reset by metamorphism above greenschist facies, either by isotopic equilibration between kerogen and carbonates, or by expulsion of light hydrocarbons from kerogen. In such circumstances, premetamorphic isotopic ratios are hard to determine without comprehensive data on the abundance and isotopic composition of both organic and carbonate carbon, to assess equilibration, and on organic hydrogen/carbon ratios, to assess hydrocarbon loss (H/C declines as hydrocarbons

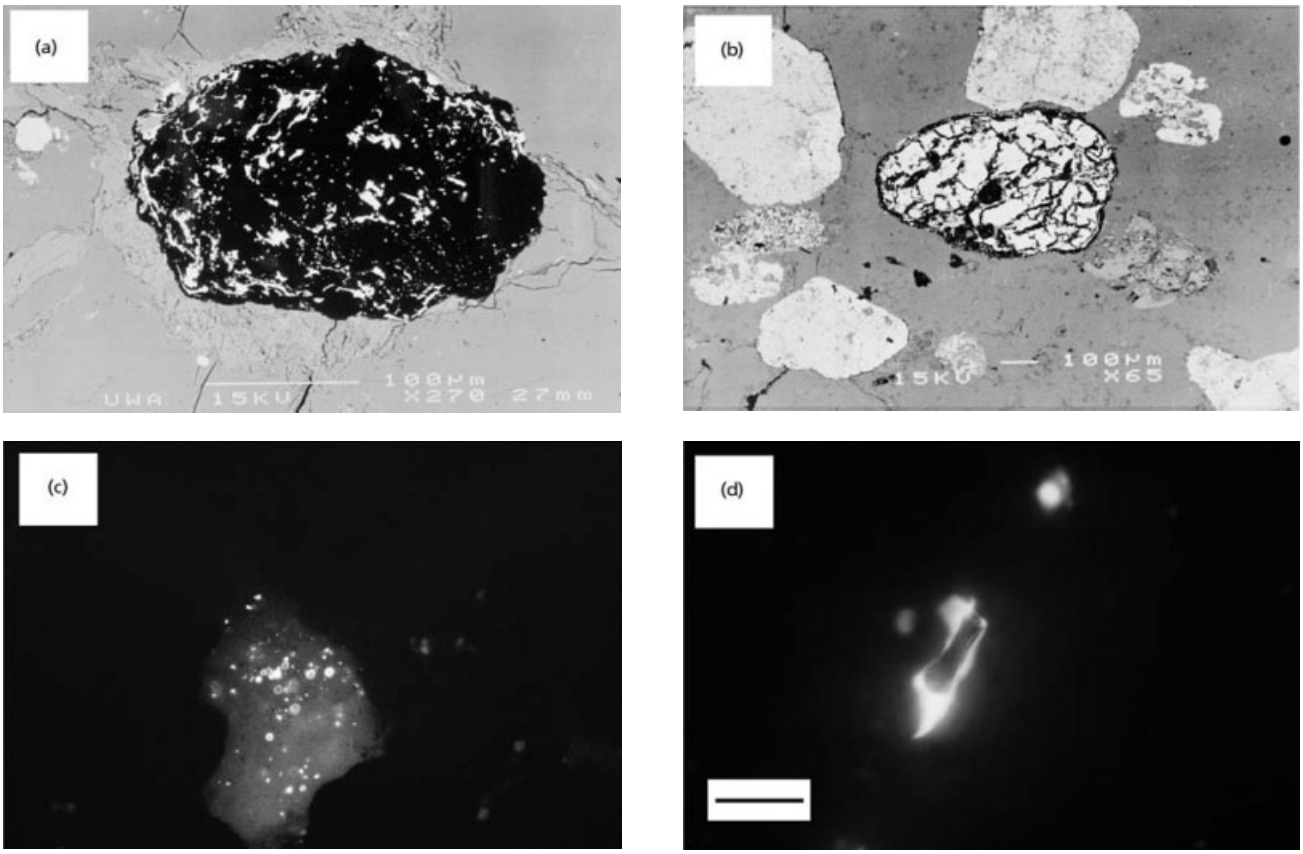


Fig. 1.1.3.5 Relics of Archaean petroleum. (a) SEM-backscattered electron (BSE) image of a bitumen nodule formed when migrating hydrocarbons were polymerized by radioactive uraninite (white), in the ≈ 2.85 Ga Elsburg Formation, Witwatersrand Supergroup, South Africa. (b) SEM–BSE image of radiogenic bitumen derived from fluid hydrocarbons infiltrating and coating a detrital uraninite grain (white), in the ≈ 3.25 Ga Mosquito Creek Formation, Australia. (c) UV-epifluorescence photo of fluorescent oil-bearing fluid inclusions in microfractures within a detrital quartz grain surrounded by black bitumen nodules, in the ≈ 2.85 Ga Elsburg Formation, Witwatersrand Supergroup, South Africa. (d) UV-epifluorescence photo of a complex oil-bearing fluid inclusion with an outer fluorescent rim of liquid oil (white) surrounding a clear gas bubble (grey), in the ≈ 2.85 Ga Elsburg Formation, Witwatersrand Supergroup, South Africa. Bar in (d) = 120 µm for (c), 10 µm for (d).

are expelled). Moreover, particularly ancient metamorphosed rocks pose special problems because abiogenic carbon could be present. Carbonaceous meteorites, primitive igneous rocks, and simulated prebiotic chemosyntheses all yield insoluble carbon with $\delta^{13}C_{org}$ values similar to metamorphosed biotic kerogen; significantly, the Itsaq metasediments were deposited at the end of an intense meteoritic bombardment. So, they might contain isotopically light carbon derived from mixed abiogenic sources which then suffered metamorphic homogenization, making it impossible to distinguish from an original biotic signature.

Whole-rock $\delta^{13}C_{org}$ values of Itsaq metasediments range from –5‰ to –28‰ (average –15‰) and it has been argued that these represent metamorphically reset photoautotrophic fractionations of biological origin (Schidlowski 1993). However, this interpretation is questionable because Itsaq $\delta^{13}C_{carb}$ values have undergone only limited resetting (their mean of –2‰ differs little from carbonates in unmetamorphosed Archaean ironstones), whereas $\delta^{13}C_{org}$ has a wide range. Moreover, ion microprobe analyses of minute graphite inclusions in apatite crystals from the Itsaq metamorphics (Mojzsis *et al.* 1996) produce markedly different isotopic results from the whole-rock studies (Fig. 1.1.3.4). These yield a unimodal population of values from Isua (>3.7 Ga) averaging –30‰ and a bimodal population from Akilia (>3.85 Ga) with a mean of –37‰ but distinct modes at –44‰ and –27‰ (Fig. 1.1.3.4a). However, it is uncertain whether these represent original isotopic signatures because there are no carbonate inclusions with which to compare them and no data allowing assessment of hydrocarbon loss. As the observed values were substantially affected by metamorphism, then the initial $\delta^{13}C_{org}$

values must have been even lighter. This would be hard to explain by biological processes other than methylotrophy which requires free oxygen (Hayes 1994), for which there is no evidence so early in Earth history. Furthermore, Rayleigh distillation of inorganic carbon during metamorphism (selective sequestration of a particular isotope in a closed system, thereby transforming the isotopic composition of the residue) could conceivably have produced graphite of the observed isotopic composition (Eiler *et al.* 1997). So, until similar data have been obtained by similar methods from similar Phanerozoic and Proterozoic rocks, perhaps judgement should be suspended on whether the carbonaceous inclusions in Greenland apatite are biogenic.

The next oldest rocks that might yield evidence of life are in the ≈3.52 Ga Coonterunah Group of Australia and Theespruit Formation of southern Africa. These have experienced mid-greenschist to lower-amphibolite facies metamorphism, about the grade where substantial isotopic resetting begins, and contain kerogen in quantities large enough to measure in whole-rock samples by conventional methods. The Theespruit Formation yields $\delta^{13}C_{org}$ values of –23‰ to –15‰ which might represent metamorphically reset autotrophic carbon, but without carbonates for comparison, such an origin remains conjecture. The Coonterunah Group contains sedimentary carbonate and kerogen, the former averaging about –2‰ and the latter about –24‰ (R. Buick and D.J. Des Marais, unpublished data). As their greenschist metamorphic grade probably did not severely affect isotopic ratios, the observed fractionation can be compared with those of younger Archaean and Proterozoic rocks and is consistent with an autotrophic origin. Thus, these rocks provide perhaps the oldest compelling evidence for life on Earth.

What were Archaean organisms like?

Archaean organisms were morphologically simple. Microfossils are spheroidal or ellipsoidal unicells that reproduced by binary fission, or filamentous chains of discoidal cells with or without cylindrical extracellular mucilaginous sheaths. As microbes are architecturally conservative, this does not necessarily imply minimal taxonomic diversity. In the modern world, a huge range of metabolic styles can lurk under the guise of a simple sphere or cylinder. So, taxonomic diversity may well have rivalled that of many modern microbial ecosystems.

Community structure was apparently also simple. Stromatolite microstructures are locally homogeneous, as are assemblages of undoubted microfossils. Benthic filaments could build mats, protecting individuals from desiccation, radiation, and erosion, and spheroids could grow in dense clusters, probably fulfilling a similar ecological function. Some mats influenced sedimentation, as bulbous, columnar, and branching stromatolites separated by mobile detrital sediment had appeared by the late Archaean.

Regardless of behaviour, organisms were small. Even late Archaean filaments were less than a few tenths of a millimetre long. Individual cells were apparently no larger than 20 μm. The thickness of the finest laminae in cherty stromatolites, where negligible compaction or recrystallization occurred, also gauges maximum cell size. Again 20 μm is the smallest measurement reported. Evidently, then, the biosphere was totally microbial.

From this, it might be inferred that the Archaean biota was also entirely prokaryotic. However, some eukaryotic algae have spheroidal vegetative cells as small as 2 μm, like those seen in the late Archaean. Although no fossils of demonstratively eukaryotic origin have ever been found in Archaean rocks, this may not mean much given the paucity of the record. A better record of the antiquity of eukaryotes may be revealed by biomarker studies.

How did Archaean organisms live?

Only a few of the many microbial metabolic strategies leave a detectable trace in the geological record. However, several of those that modulate biogeochemical cycles had already evolved by the late Archaean.

Photoautotrophy is the dominant form of carbon fixation on Earth today and thus controls the flow of energy through the biosphere. The process imparts a ≈25‰ isotopic fractionation between the carbon source and the organic product, varying somewhat according to the metabolic pathway, nutrient supply, carbon availability, and ambient temperature. Such a fractionation is evident in 3.52 Ga rocks of the Coonterunah Group. Coupled with the presence of structures in the 3.46 Ga Warrawoona Group that are best interpreted as stromatolites accreted by phototropic organisms, this strongly suggests that photoautotrophy had arisen by then. Further, there is presumptive isotopic evidence in the >3.7 Ga Itsaq metasediments for earlier establishment of this metabolic process, although the severity of the metamorphic overprint makes this interpretation equivocal.

Oxygenic photosynthesis is a form of photoautotrophy which is generally thought, on molecular phylogenetic grounds, to have arisen late in metabolic evolution. The only microbes that use this metabolic pathway are the cyanobacteria, some of which are morphologically distinctive. Though globular objects from the <3.46 Ga Apex Basalt have been interpreted as sheath-enclosed spheroidal colonies of cyanobacteria (Schopf and Packer 1987), these are either not fossils or not old. None of the well-preserved late Archaean microfossils is morphologically diagnostic of cyanobacteria;

all may be the remains of anoxygenic bacteria. It is not until ≈2.0 Ga that the first indisputable cyanobacterial fossils (*Eoentophysalis*) appear in the record.

Biological activity in environments lacking exogenous sources of reducing power provides indirect evidence for the advent of oxygenic photosynthesis (Buick 1992). In the 2.72 Ga Tumbiana Formation, Australia, a diverse stromatolite assemblage with palimpsests of phototropic filamentous microbes (Fig. 1.1.3.2) developed in sulphur-deficient lakes on flood basalts. Without allochthonous organic matter or hydrocarbons available, the local ecosystem was necessarily based on autotrophy. This must have been photosynthetic, because oxidized compounds for anaerobic respiration were evidently scarce. As the carbonate phase precipitating in the lakes was calcite rather than siderite, conditions were apparently not highly reducing, so molecular hydrogen was probably not abundant. Thus, anaerobic photosynthesis cannot have been the sole metabolic energy source powering the whole ecosystem and oxygenic photosynthesis must have been employed.

The same lake sediments have extremely light $\delta^{13}C_{org}$ values, −40‰ to −60‰, indicating that primary production was recycled by methanogenic and methylotrophic microbes (Hayes 1994). The former produce methane further depleted in ^{12}C, whereas the latter consume it. This also implies the existence of oxygenic photosynthesis, as methylotrophy requires molecular oxygen. These particular pathways probably prevailed because the local scarcity of oxidized substrates inhibited other forms of organic recycling (Buick 1992).

In modern marine environments, organic recycling is generally dominated by bacterial sulphate reduction. Though sulphate was abundantly available in some early Archaean evaporative environments, the very large (>20‰) whole-rock isotopic fractionations clearly indicative of this pathway are not obvious in the geological record until the early Proterozoic. As early as ≈3.4 Ga, however, micron-scale laser-ablation analyses of sedimentary pyrites reveal small but significant (10–15‰) $\delta^{34}S$ spreads. These may record microbial sulphate reduction where high ocean temperatures promoted high sulphate reduction rates, inducing negligible isotopic fractionations (Ohmoto *et al.* 1993). But the proposed temperature increase (30–40°C above present) is incompatible with the Archaean evaporite record, where relics of gypsum instead of anhydrite indicate rather cooler conditions. Moreover, biological sulphate reduction almost always produces large fractionations in experimental studies, regardless of reaction rate. So, until control studies using laser ablation on more modern biogenic pyrite formed under the proposed primordial conditions show similar isotopic spreads, the Archaean origin of bacterial sulphate reduction must remain speculative.

The early evolution of nitrogen metabolism is poorly known. The few available data suggest that $\delta^{15}N$ values of sedimentary organic matter, now +2‰ to +10‰, were lighter in the Archaean, down to −6‰ (Beaumont and Robert 1999). As the heavier modern values result from isotopic fractionation accompanying microbial denitrification of nitrate to molecular nitrogen, biological nitrification and denitrification were perhaps insignificant processes in suboxic Archaean environments. Regardless, biological nitrogen fixation must have already evolved because fixed inorganic nitrogen would have been scarce in such conditions.

Where did Archaean organisms live?

Contrary to popular belief, a wide environmental range is represented in the early geological record. By the end of the Archaean, life occupied many of these habitats, constraining the ecological tolerances of ancient organisms.

Benthic organisms flourished throughout the marine photic zone, indicated by the abundance of stromatolites in intertidal, shallow subtidal, and shelf settings. In the Transvaal Supergroup, South Africa, filamentous microbial mats grew at depths up to 50 m in an outer shelf to basin environment (Klein *et al.* 1987). Matting microbes could withstand considerable current energies, as Archaean stromatolites are frequently elongated with asymmetric ripples occupying intervening spaces. However, current activity was not a prerequisite for their existence, as cuspate stromatolites in the Transvaal Supergroup evidently grew below wave base under conditions of negligible water movement (Sumner 1997). Mat-forming organisms could tolerate a wide range of salinities, from normal marine through carbonate (Sumner 1997) to sulphate saturation (Buick *et al.* 1981), judging from the evaporite minerals precipitated during stromatolite formation.

Marine plankton was presumably also common, because basinal kerogenous shales are widespread and abundant. These have such high organic carbon contents (up to 165 mg/g), even after diagenetic and metamorphic decarbonation, that it is extremely unlikely that benthic production alone could have fixed so much carbon at such depths. However, no plausible microfossils have ever been found in Archaean shales.

Both benthic and planktic organisms also inhabited non-marine aqueous environments. Diverse stromatolites occur in lacustrine facies of the 2.72 Ga Tumbiana Formation, Australia, some interbedded with halite moulds indicating hypersaline conditions (Buick 1992). Their constructing microbes could withstand very high sedimentation rates as they incorporate thick lenses and laminae of volcanic ash, implying either rapid motility or high growth rates. Similar stromatolites occur in

similar settings in the Ventersdorp Supergroup, South Africa, which is of similar age. Lacustrine basinal shales associated with both of these stromatolite suites are highly kerogenous, so plankton evidently existed in non-marine water bodies as well as in the ocean.

It is unclear whether terrestrial surfaces were inhabited during the Archaean, as preservation is improbable in such settings. In the modern world, photosynthetic bacteria colonize rock and soil surfaces, especially in moist places, forming opportunistically viable crusts. Photosynthesizers also occupy pore spaces within rocks and soils as far as light penetrates. In the absence of an oxygenic atmosphere with an ozone shield, UV fluxes may have been too high for bacterial survival on exposed surfaces, but endolithic or soil-dwelling organisms might have thrived. Palaeosols in the 2.77 Ga Mt Roe Basalt, Australia, contain isotopically light kerogen which has been interpreted as the remains of terrestrial organisms (Rye 1998). However, the organic material is concentrated in fragments filling apparent erosion channels, so a terrestrial origin has yet to be demonstrated.

Phylogenetic studies of modern bacteria suggest that many of the most primitive organisms are thermophilic. However, it is difficult to determine whether the Archaean biota reflected this tendency. The marine oxygen isotope geothermometer—the most effective measure of palaeotemperatures in the later Phanerozoic—is unreliable if seawater $\delta^{18}O$ has evolved through time. Moreover, many Archaean cherts are hydrothermally silicified volcanogenic and evaporitic sediments, so their $\delta^{18}O$ values do not record ambient seawater temperatures. A better constraint is provided by evaporitic parageneses, in which the precipitation of either gypsum or anhydrite as the sulphate phase is governed by temperature. Voluminous evaporites, pseudomorphous after gypsum, are associated with the >3.46 Ga probable stromatolites at North Pole, Australia, indicating temperatures of ≈57°C if sea water had no NaCl, or less if sea water was saline. As halite moulds occur in other early Archaean sedimentary rocks, it seems likely that the earliest microbial communities evident in the fossil record were not dominated by thermophiles. So, as early as ≈3.5 Ga, the microbial world had evidently evolved beyond the state exemplified by the lowest branches of the tree of life.

References

Altermann, W. and Schopf, J.W. (1995) Microfossils from the Neoarchean Campbell Group, Griqualand West Sequence of the Transvaal Supergroup, and their paleoenvironmental and evolutionary implications. *Precambrian Research* **75**, 65–90.

Awramik, S.M., Schopf, J.W. and Walter, M.R. (1983) Filamentous fossil bacteria from the Archean of Western Australia. *Precambrian Research* **20**, 357–374.

Beaumont, V. and Robert, F. (1999) Nitrogen isotope ratios of kerogens in Precambrian cherts: a record of the evolution of atmosphere chemistry? *Precambrian Research* **96**, 63–82.

Buick, R. (1992) The antiquity of oxygenic photosynthesis: evidence from stromatolites in sulphate-deficient Archaean lakes. *Science* **255**, 74–77.

Buick, R., Dunlop, J.S.R. and Groves, D.I. (1981) Stromatolite recognition in ancient rocks: an appraisal of irregularly laminated structures in an early Archaean chert-barite unit from North Pole, Western Australia. *Alcheringa* **5**, 161–181.

Dutkiewicz, A., Rasmussen, B. and Buick, R. (1998) Oil preserved in fluid inclusions in Archaean sandstones. *Nature* **395**, 885–888.

Eiler, J.M., Mojzsis, S.J. and Arrhenius, G. (1997) Carbon isotope evidence for early life. *Nature* **386**, 665.

Grotzinger, J.P. and Rothman, D.H. (1996) An abiotic model for stromatolite morphogenesis. *Nature* **383**, 423–425.

Hayes, J.M. (1994) Global methanotrophy at the Archean–Proterozoic transition. In: S. Bengtson, ed. *Early life on Earth*, pp. 220–236. Columbia University Press, New York.

Hayes, J.M., Kaplan, I.R. and Wedeking, K.W. (1983) Precambrian organic geochemistry: preservation of the record. In: J.W. Schopf, ed. *Earth's earliest biosphere: its origin and evolution*, pp. 93–134. Princeton University Press, Princeton.

Klein, C., Beukes, N.J. and Schopf, J.W. (1987) Filamentous microfossils in the early Proterozoic Transvaal Supergroup: their morphology, significance, and paleoenvironmental setting. *Precambrian Research* **36**, 81–94.

Lanier, W.P. (1986) Approximate growth rates of Early Proterozoic microstromatolites as deduced by biomass productivity. *Palaios* **1**, 525–542.

Lowe, D.R. (1994) Abiological origin of described stromatolites older than 3.2 Ga. *Geology* **22**, 387–390.

Mojzsis, S.J., Arrhenius, G., McKeegan, K.D., Harrison, T.M., Nutman, A.P. and Friend, C.R.L. (1996) Evidence for life on earth before 3,800 million years ago. *Nature* **384**, 55–59.

Ohmoto, H., Kakegawa, T. and Lowe, D.R. (1993) 3.4-billion-year-old biogenic pyrites from Barberton, South Africa: sulfur isotope evidence. *Science* **262**, 555–557.

Rye, R. (1998) Highly negative $\delta^{13}C$ values in organic carbon in the Mt. Roe #2 paleosol: terrestrial life at 2.765 Ga? *Mineralogical Magazine* **62A**, 1308–1309.

Schidlowski, M. (1993) The initiation of biological processes on Earth: summary of empirical evidence. In: M.H. Engel and S.A. Macko, eds. *Organic geochemistry*, pp. 639–655. Plenum Press, New York.

Schopf, J.W. and Packer, B.M. (1987) Early Archean (3.3-billion to 3.5-billion-year-old) microfossils from Warrawoona Group, Australia. *Science* **237**, 70–73.

Schopf, J.W. and Walter, M.R. (1983) Archean microfossils: new evidence of ancient microbes. In: J.W. Schopf, ed. *Earth's earliest biosphere: its origin and evolution*, pp. 214–239. Princeton University Press, Princeton.

Sumner, D.Y. (1997) Late Archean calcite–microbe interactions: two morphologically distinct microbial communities that affected calcite nucleation differently. *Palaios* **12**, 302–318.

Walsh, M.M. (1992) Microfossils and possible microfossils from the Early Archean Onverwacht Group, Barberton Mountain Land, South Africa. *Precambrian Research* **54**, 271–293.

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1.1.4 Late Proterozoic Biogeochemical Cycles

G.A. LOGAN and R.E. SUMMONS

Introduction

The Proterozoic Eon (2500–540 Ma) saw episodic increases in atmospheric oxygen, the evolution of multicellular life, and at its close, an enormous radiation of animal diversity. The rise of metazoans is marked by the Ediacara fauna (see Section 1.2.1), with body fossils evident in sediments as old as 594 Ma, i.e. the end of the last Varanger glaciation. Evidence for metazoan activity is also present in the trace fossil record. Simple burrows and traces indicate sediment processing, and hence the development of a through gut. Zooplankton have not yet been identified in sediments from this period but it seems likely that water column grazers would also have utilized a through gut. This evolutionary innovation is potentially important for the course of biogeochemical cycles; its first appearance provided a significant additional mechanism for reprocessing organic matter and nutrients found in phytoplankton and transferring the residues out of the photic zone down to the sea floor, in the form of fast-sinking faecal pellets. Furthermore, sediment agitation, or bioturbation related to metazoan feeding and movement, would have affected porewater chemistry and nutrient distribution in surface sediments, which, in turn, would have altered the composition of bacterial communities and early diagenesis (Aller 1982).

Sediments spanning the Neoproterozoic to Early Cambrian preserve several geochemical signals which appear to reflect these biological changes. These include a reordering of the $\delta^{13}C$ relationship between kerogen (insoluble organic matter) and co-occurring bitumen (organic matter soluble in organic solvents), a marked increase in the abundance of phosphorites, and a depletion in $\delta^{34}S$ of diagenetic pyrite. All these changes appear to be related to a major reorganization in biogeochemical cycles of carbon, phosphorus, and sulphur (Logan *et al.* 1995) and, as a consequence, in the distribution of these elements and their isotopes in the biosphere and geosphere. These geochemical signals are important because they record evidence of changing biological activity and environmental parameters independent of sediment lithologies and the occurrence of visible fossils.

Impact of animal activity on organic matter

The carbon isotopic composition of co-occurring kerogen and bitumen has been extensively studied in Phanerozoic and Proterozoic sediments, in the course of research to establish the origin and migration history of petroleum. Phanerozoic kerogen is enriched in ^{13}C relative to associated bitumen, unless contamination or hydrocarbon migration has affected the samples. Early studies of Proterozoic organic matter showed the reverse—unlike Phanerozoic material, the bitumen could be enriched in ^{13}C relative to associated kerogen in some samples. Based on experience with Phanerozoic organic matter, these data were originally dismissed as the result of migration contamination (Hoering 1965). This enigma has been resolved by recent developments in analytical techniques. The availability of gas chromatography-combustion-isotope ratio monitoring mass spectrometry (GC-C-IRMS) instruments has allowed the measurement of $\delta^{13}C$ compositions for individual compounds that comprise complex mixtures such as bitumen. When applied to Proterozoic sediments with reliable pedigrees, it was found that only certain compounds, specifically the *n*-alkanes, were enriched in ^{13}C relative to associated kerogen (Logan *et al.* 1995, 1997). Thus, the unusual isotopic relationship observed in Proterozoic kerogens indicates that Phanerozoic kerogens must be fundamentally different in make-up. A specific source of ^{13}C-enriched *n*-alkanes that is dissimilar to the bulk of original TOC (total organic carbon) is required to explain the difference. These compounds are generally derived from cell wall lipids and fat stores within plants and bacteria. To explain why Proterozoic bitumen, and *n*-alkanes in particular, could be selectively enriched in ^{13}C, a new model was developed (Logan *et al.* 1995).

As a consequence of isotopic fractionation in the pathways leading to their biosynthesis, lipids are depleted in ^{13}C relative to total cell carbon. They are also depleted relative to the proteins and carbohydrates comprising the bulk of carbon in those cells. Lipid moieties in Phanerozoic kerogen also tend to be depleted in ^{13}C relative to TOC even after burial, diagenesis, and petroleum generation. However, hydrocarbons can approach the $\delta^{13}C$ composition of the kerogen as hydrocarbon generation progresses (Eglinton 1994). Generally, the bulk of organic matter preserved in kerogen is thought to comprise the most recalcitrant products of photosynthetic activity. A major component has been identified chemically and microscopically as algaenan, an aliphatic biopolymer, which is thought to produce the bulk of *n*-alkanes that eventually find their way into petroleum.

Selective ^{13}C-enrichment occurs as a proportion of carbon is metabolically reprocessed through food chains in what is called 'heterotrophic enrichment' (Hayes 1993). This process leads to the organisms at higher trophic levels becoming increasingly enriched

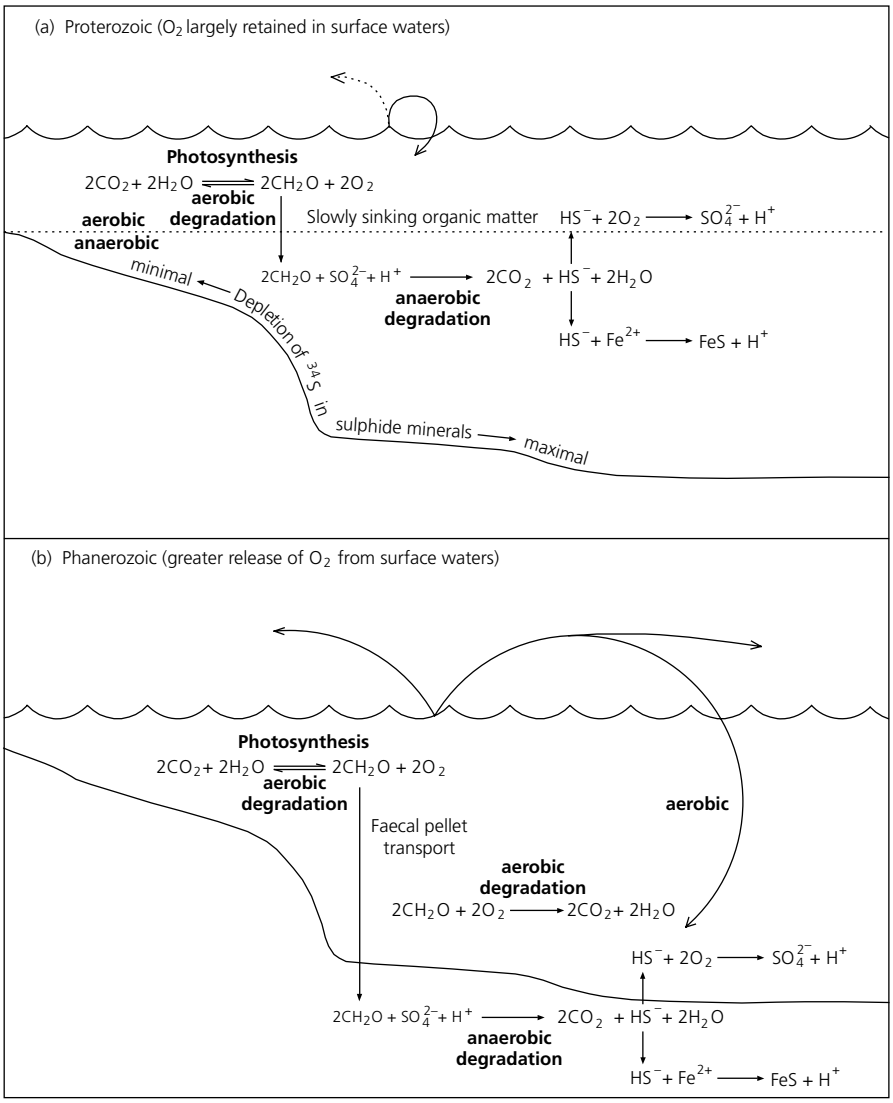

(a) Proterozoic (O_2 largely retained in surface waters)
Photosynthesis
$2CO_2 + 2H_2O \rightleftharpoons 2CH_2O + 2O_2$
aerobic degradation
aerobic
anaerobic
Slowly sinking organic matter
$HS^- + 2O_2 \rightarrow SO_4^{2-} + H^+$
$2CH_2O + SO_4^{2-} + H^+ \rightarrow 2CO_2 + HS^- + 2H_2O$
anaerobic degradation
$HS^- + Fe^{2+} \rightarrow FeS + H^+$
minimal
Depletion of ^{34}S in sulphide minerals
maximal
(b) Phanerozoic (greater release of O_2 from surface waters)
Photosynthesis
$2CO_2 + 2H_2O \rightleftharpoons 2CH_2O + 2O_2$
aerobic degradation
Faecal pellet transport
aerobic
aerobic degradation
$2CH_2O + 2O_2 \rightarrow 2CO_2 + 2H_2O$
$HS^- + 2O_2 \rightarrow SO_4^{2-} + H^+$
$2CH_2O + SO_4^{2-} + H^+ \rightarrow 2CO_2 + HS^- + 2H_2O$
anaerobic degradation
$HS^- + Fe^{2+} \rightarrow FeS + H^+$

Fig. 1.1.4.1 (a) Slow-sinking organic matter is degraded in the upper water column and acts as an oxygen sink, leading to low oxygen levels in deeper waters. (b) Fast-sinking particles remove organic matter from the photic zone, increasing oxygen availability. This oxygen-enriched water ventilates deeper waters and forces anaerobic activity into the sediment pile.

in ^{13}C. An absence of grazing zooplankton during most of the Proterozoic would result in much photosynthetic organic carbon sinking more slowly through the water column (Logan *et al*. 1995). This organic matter, if not adsorbed on to fast-sinking mineral particles or confined within faecal pellets, would be more prone to bacterial reprocessing. This would lead to a relative enrichment of the preserved carbon in lipids derived from later stage heterotrophic bacteria. These lipids, enriched in ^{13}C, could have provided the source of *n*-alkanes in Proterozoic bitumen. This model incorporates a testable hypothesis. In Proterozoic shallow water environments, where sediment settling times were shorter, the bitumen fraction of TOC should not be as enriched relative to the kerogens as it would in sediments from deeper waters. This was shown to be the case in sediments from the Bitter Springs Formation (Logan *et al*. 1997).

Implications of the impact of animals on biogeochemical cycles

A significant proportion (in some cases up to 66%) of bioavailable carbon currently reaches the abyssal sea floor in the form of fast-sinking faecal pellets (e.g. Pilskaln and Honjo 1987). Accordingly, a number of significant observations follow from the hypothesis that the first arrival of coelomate metazoans introduced a new mechanism for removing phytoplankton debris from the photic zone. Oxygen concentrations within the surface ocean could only increase in proportion to organic carbon which escaped remineralization by removal from the photic zone (Fig. 1.1.4.1a). As the surface ocean oxygen sink, provided by decaying phytoplankton, decreased by more rapid transfer of labile organic matter to deeper waters, a net increase in oxygen availability in the photic zone occurred. In turn, down-

welling of these oxygen-enriched surface waters increased oxygen availability in the deeper ocean (Fig. 1.1.4.1b).

The repackaging of phytoplankton debris would also have affected the distribution of nutrients and trace elements in the water column and in the surface sediments. Phosphate is a vital nutrient for life and, along with nitrate, it limits biological production in the oceans. However, unlike nitrate, phosphate cannot be generated directly in an environment. Its distribution is linked to transport mechanisms, and to tectonic cycles and the weathering of granites (Cook 1992). This means that, over geological time periods, phosphorus is a limiting nutrient for primary productivity. Therefore, the observed switch from low levels of phosphorite formation during most of the Proterozoic, to massive and abundant phosphoritic sediments by Early Cambrian times (Cook 1992) is of great significance. The precipitation of phosphorus occurs under quite specific redox conditions, requiring aerobic environments in order to complex with iron hydroxides. Certain bacteria also fix phosphorus under aerobic conditions and consume it during periods of anoxia. This leads to a strong coupling between phosphorus and oxygen in the Phanerozoic (Van Cappellen and Ingall 1994). In the absence of fast-sinking particles, nutrients such as phosphorus and nitrate would have been recycled rapidly by decay within the photic zone maintaining a strong 'nutrient trap'. Any biological innovation which caused nutrient-rich primary organic matter to be rapidly removed from the photic zone would have broken this 'nutrient trap'. At the same time that oxygen availability was rising in deeper waters, phosphorus transfer also increased, and a labile supply of organic matter was added at the sediment–water interface.

Increased levels of labile, nutrient-rich organic matter at the sediment–water interface, coupled with increased oxygen availability within the lower water column, would have provided a stimulus to benthic communities (see Section 1.2.3). This organic matter would be a rich food source not only for benthic metazoans but also for sedimentary bacterial communities. This combination of bacterial activity and bioturbation directly affects porewater chemistry (Aller 1982). Injection of oxygen during bioturbation would have forced anaerobic bacteria deeper into the sediment pile and created more variable and fluctuating redox conditions close to the sediment–water interface.

Sulphate-reducing bacteria use seawater sulphate to oxidize organic matter; during this process the sulphide produced is depleted in ^{34}S relative to the sulphate used. In pure bacterial culture, depletions in ^{34}S range from 4 to 46‰, with an average of 18‰; in Phanerozoic marine sediments depletions range from 24 to 71‰, with an average of 51‰ (Canfield and Teske 1996). This means that sulphate-reducing bacteria are not solely responsible for the ^{34}S depletions seen in Phanerozoic sediments. It is currently hypothesized that sulphide-oxidizing bacteria may be responsible for the observed shift in the sulphate–sulphide isotopic relationship at some time prior to the Cambrian (Canfield and Teske 1996). Sulphide-oxidizing bacteria, such as *Beggiatoia* or *Thioploca*, have specific environmental tolerances and require both hydrogen sulphide and oxygen.

Proterozoic marine sulphides are generally enriched in ^{34}S compared with Phanerozoic sulphides (Canfield and Teske 1996). If sulphate supplies are limited during sulphate reduction, the isotopic composition of the total sulphide gradually approaches that of the starting sulphate. Therefore, if porewater sulphate is completely consumed, the isotopic composition of the sulphide produced will be the same as the starting material. Without bioturbation, Proterozoic porewaters would have become rapidly anoxic just below the sediment–water interface due to low oxygen concentrations and low levels of replenishment. Sulphate within porewaters would also not be replenished and $\delta^{34}S$ compositions of pyrite would approach that of coeval seawater sulphate as sulphate-reducing bacteria consumed sulphate at the expense of sedimentary organic matter. Evidence exists for a shift in the isotopic composition of some Proterozoic sulphides between 1.0 and 0.6 Ga, but a fundamental shift appears to occur around the Proterozoic–Cambrian boundary (Canfield and Teske 1996). This implies that a change in the supply of both oxygen and sulphide occurred in sediments around the boundary. A plausible explanation is that increased levels of bioturbation allowed greater mixing of porewaters and hence development of sulphide-oxidizing communities within marine sediments which, in turn, led to a general ^{34}S depletion in pyrite.

Conclusion

The major radiation of animals just prior to the Cambrian appears to be linked to contemporaneous changes in several geochemical signals. The advent of fast-sinking particles, such as faecal pellets, led to a change in the flux of labile carbon out of the photic zone, affecting oxygen availability throughout the water column. This new rapid transport of organic matter also affected its preservation by decreasing settling time, and thus reducing its availability to bacterial attack in the water column. Its nutrient-rich labile character would also have acted as a carbon and energy source for both benthic metazoan and bacterial communities. Increased oxygen concentrations in deeper waters, coupled with this enhanced food supply, stimulated bioturbation, which would have affected redox conditions close to the sediment–water interface. Changes in the redox condi-

tions impacted on sedimentary bacteria and on early diagenetic mineral precipitation, such as phosphorites and sulphides. The radiation of zooplankton and benthic metazoans had a profound effect on the environment, and this event is recorded in isotopic and other evidence of changes in biogeochemical cycles.

References

Aller, R.C. (1982) The effects of macrobenthos on chemical properties of marine sediments and overlying water. In: P.L. McCall and M.J.S. Tevesz, eds. *Animal–sediment relations*, pp. 53–102. Plenum, New York.

Canfield, D.E. and Teske, A. (1996) Later Proterozoic rise in atmospheric oxygen concentration inferred from phylogenetic and sulphur-isotope studies. *Nature* **382**, 127–132.

Cook, P.J. (1992) Phosphogenesis around the Proterozoic–Phanerozoic transition. *Journal of the Geological Society of London* **149**, 615–620.

Eglinton, T. (1994) Carbon isotope evidence for the origin of macro-molecular aliphatic structures in kerogen. *Organic Geochemistry* **21**, 721–735.

Hayes, J.M. (1993) Factors controlling ^{13}C contents of sedimentary organic compounds: principles and evidence. *Marine Geology* **113**, 111–125.

Hoering, T.C. (1965) The extractable organic matter in Precambrian rocks and the problem of contamination. *Carnegie Institute Year Book* **64**, 215–218.

Logan, G.A., Hayes, J.M., Hieshima, G.B. and Summons, R.E. (1995) Terminal Proterozoic reorganization of biogeochemical cycles. *Nature* **376**, 53–56.

Logan, G.A., Summons, R.E. and Hayes, J.M. (1997) An isotopic biogeochemical study of Neoproterozoic and early Cambrian sediments from the Centralian Superbasin, Australia. *Geochimica et Cosmochimica Acta* **61**, 5391–5409.

Pilskaln, C.H. and Honjo, S. (1987) The fecal pellet fraction of biogeochemical particles to the deep sea. *Global Biogeochemical Cycles* **1**, 31–48.

Van Cappellen, P. and Ingall, E.D. (1994) Redox stabilization of the atmosphere and oceans by phosphorus-limited marine productivity. *Science* **271**, 493–496.

1.2 The Cambrian Radiation

1.2.1 Metazoan Origins and Early Evolution

D.H. ERWIN

Introduction

The nature of the origin and early evolution of animals remains among the great conundrums of the history of life, despite incredible advances over the past decade. New fossil discoveries, a dramatically improved time scale, exciting new views of the relationships between major metazoan groups based on both molecular and morphological data, and a wealth of information from comparative studies of the developmental process have all contributed to our growing understanding of events during the late Neoproterozoic and earliest Cambrian (about 610–530 Ma).

Precise absolute age dating has recently provided the first reliable temporal framework for the evolution of early metazoans during the Neoproterozoic, the soft-bodied fossils of the Ediacaran assemblage, and the beginning of the Early Cambrian radiation. There is a continuing debate, however, over whether the origin of animals substantially predates their appearance in the fossil record. Such views have received impetus from molecular clock studies that may suggest a relatively early origin of the clade, relative to its appearance in the fossil record. An increasing diversity of molecular data has rejuvenated the issue of metazoan phylogeny, a once moribund field. The relative roles of environmental and developmental changes in precipitating the early phase of animal evolution are important areas of research.

Earliest history (?) of metazoans

The metazoan lineage diverged from a single-celled eukaryote, probably a choanoflagellate, about 1000 Ma, during the Proterozoic. This divergence occurred during a radiation of a number of higher eukaryotic groups, including plants and fungi, although there is considerable uncertainty about its timing. Reports of metazoans prior to about 610 Ma occur with some frequency, but none has been generally accepted by palaeontologists.

Given the significance that would be attached to undisputed pre-600 Ma metazoans, it is hardly surprising that such claims are subject to considerable scrutiny, and their proponents must advance substantial evidence in their favour. One difficulty is distinguishing possibly biogenic structures from inorganic structures, and metazoans from algae or other non-metazoan fossils. Some of these reports are intriguing, and evidence of metazoans before 600 Ma may yet appear.

Among claims for early metazoans are a group of narrow, seemingly annulated filaments from China, poorly dated to about 700–800 Ma, including *Sinosabellidites* and *Protoarenicola*. The lack of well-preserved structures and living analogues makes these difficult to assign to any group, algal or metazoan (Sun 1994). A variety of purported trace fossils has also been reported, including 1000 Ma worm burrows from India, several unusual forms from the Belt sequence of Wyoming (USA), and the supposed feeding trace *Brooksella canyonensis* from the 1000+ Ma Grand Canyon Series. None of these has yet been accepted as of metazoan origin. Other evidence which has been advanced to suggest the presence of metazoans prior to about 600 Ma includes molecular analyses (discussed below), possible faecal pellets (requiring an anus, and thus a relatively complex organism), and a decline in the diversity and abundance of stromatolites. Each of these lines of reasoning has become increasingly difficult to sustain (see also Section 3.4.2).

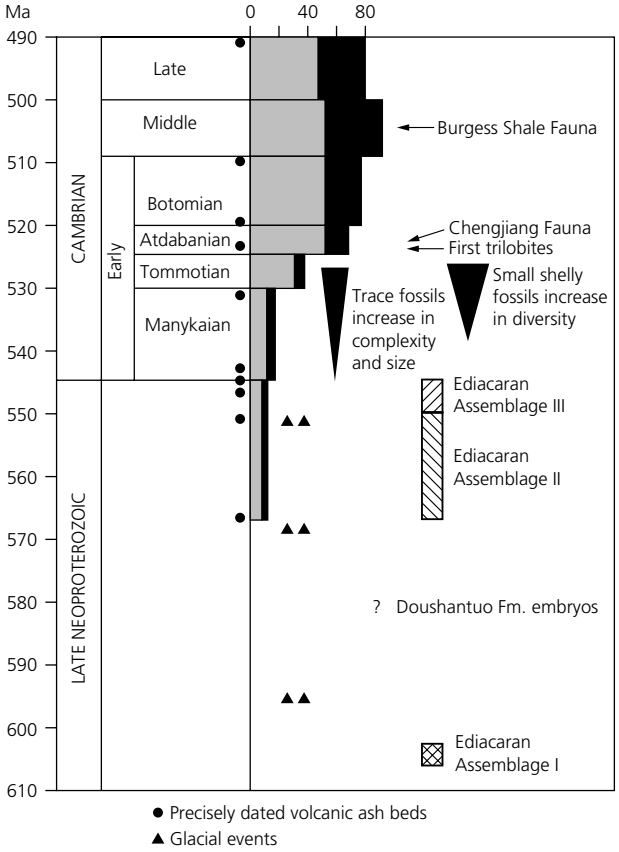


Fig. 1.2.1.1 Geological and biological events of the late Neoproterozoic and Cambrian, based on recent geochronological data. The grey and black boxes show the increasing diversity of marine metazoan orders and classes, respectively, based on data from Sepkoski (after Grotzinger *et al.* 1995). Ediacaran assemblages I, II, and III are of increasingly higher diversity and complexity. Assemblage I is known only from the Mackenzie Mountains of Canada.

Ediacaran metazoans

The late Neoproterozoic was an interval of substantial geological activity, including glaciations, rapid geochemical changes, and pervasive tectonic movements. Many workers have suggested that these events triggered the metazoan radiation. Establishing a causal connection, however, between the environmental changes and the biotic events remains difficult. Remarkable changes in carbon isotopes, often correlated with glacial sediments, suggest several discrete glacial episodes during this interval (Fig. 1.2.1.1; Kaufman *et al.* 1997). One of these, best recorded in the Windermere Supergroup of the Mackenzie Mountains of Canada, is dated to about 600 Ma and overlies a suite of simple discs and rings that may record the earliest assemblage of metazoans. Evidence of a possible second ice age occurs higher in the section following the initial diversification of the Ediacaran fauna (described below), but before the most diverse Ediacaran assemblage. These isotopic shifts suggest substantial changes in the carbon cycle, but the link to evolutionary innovations is unclear. Fortunately, since the unicellular fossils of this interval have limited biostratigraphic utility between different continental regions, the isotopic changes have proved to be of great value for correlation between regions (Kaufman *et al.* 1997).

The Ediacaran fossils form the most notable part of the late Neoproterozoic fossil record. First discovered in rocks from Namibia and Newfoundland, this assemblage of soft-bodied organisms was named for a locality in the Ediacaran Hills of South Australia and has now been recovered from more than 30 localities around the world. The Ediacaran fossils were initially assigned to the Cambrian, until overwhelming evidence demonstrated that they underlie the first skeletonized fossils. Until recently they were generally dated at 620–680 Ma, with the base of the Cambrian at 570–590 Ma. Thus a lengthy, unfossiliferous gap was believed to occur between the Ediacaran fossils and the radiation of skeletonized and other fossils at the base of the Cambrian. This gap has vanished with the application of high-precision dating of the mineral zircon, which incorpor-

ates uranium when it is formed during volcanic eruptions, and has allowed the development of a far more precise time scale for Neoproterozoic events than was previously available (see also Section 5.4.2).

The Ediacaran assemblage includes a spectrum of morphologies, many of which seem unfamiliar, even bizarre, to modern eyes. The earliest fossils are the simple discs from the Twitya Formation in the Mackenzie Mountains; although they have not been found in other areas, this assemblage has been characterized as Ediacaran Assemblage I (Narbonne *et al.* 1994). Dating to about the same time are trace fossils which may have faecal strings. This is importance evidence, for it suggests that a complete gut (with an anus) was present in these bilaterians. Sponges are known to have evolved by this time. The remaining localities of Ediacaran fossils are dated to the last 20 million years of the late Neoproterozoic. These successively more diverse assemblages include fronds as much as 1 m long, seemingly segmented forms, and discs.

The affinities of Ediacaran forms are unknown—or rather the affinities are well known to individual experts, each of whom has a different opinion. Some workers believe that the fossils form a single, monophyletic assemblage that has been described variously as an extinct animal-like clade, the Vendozoa, possibly photosynthetic or chemosynthetic (Seilacher 1992), as relatives of the Cnidaria, as lichens, or as protists. Other workers view the Ediacaran fossils as phylogenetically diverse, possibly including members of the Cnidaria, Annelida, Arthropoda, Mollusca, and even Echinodermata. The more diverse assemblages are known as Assemblage II, which is replaced by the high-diversity Assemblage III for the last few million years of the late Neoproterozoic. Clearly defined mouths are absent from Ediacarans (*Kimberella* may be an exception: Fedonkin and Waggoner 1997) and there are few useful characters for phylogenetic analysis. *Swartpuntia,* recently described from Namibia (Narbonne *et al.* 1997), is frond-like with multiple vanes attached to a central stalk, similar to *Pteridinium*. But it is also seemingly segmented, much like *Dickinsonia.* While the combination of characters is useful in linking two morphologically disparate groups, they also confound the issue of the overall affinities of the assemblage. The group including *Dickinsonia*, *Pteridinium*, and now *Swartpuntia* was characterized by Seilacher (1992) as having a unique quilted construction, much like an air mattress. The members of this group are probably more closely related to each other than to other Ediacaran fossils.

The rocks of the Kuibis and Schwarzrand subgroups in the southern Namibian desert have been the key to resolving the Neoproterozoic time scale. Hundreds of square kilometres of outcrop have yielded a detailed record of the sedimentological, geochemical, and palaeontological changes through the late Neoproterozoic. Of particular significance is a number of volcanic ash beds interbedded with Ediacaran fossils, trace fossils, and rocks amenable to stable isotope studies. The Namibian sections also contain the earliest skeletal fossils, the tube *Cloudina*, and other small shelly fossils. U/Pb dating of the mineral zircon has allowed geologists to place the biotic and environmental changes within a firm temporal framework. The diverse Ediacaran Assemblage III is younger than 549 Ma, and carbon isotope chemostratigraphy suggests that this is true globally (Grotzinger *et al.* 1995). Moreover, some of the Ediacaran fossils are as young as 543 Ma, essentially the same age as the Cambrian boundary as dated in Siberia and elsewhere. Thus the diverse Ediacaran fossils are far younger than previously believed, and there is no lengthy gap between the Ediacaran fossils and the onset of the Cambrian. Moreover, *Cloudina* and the other shelly fossils suggest an element of continuity with the growing diversity of shelly fossils during the overlying Manykaian Stage of the Early Cambrian (Grotzinger *et al.* 1995).

The preservation of the Ediacaran fossils is unusual and remains incompletely understood. Soft-bodied fossils are rarely preserved, but this assemblage has been found in both deep- and shallow-water settings, most commonly as sole marks on the bottom of event beds, indicating rapid deposition. That apparently soft-bodied organisms can survive these storm events without marked injury suggests that they were relatively tough. Some workers have also suggested that the sediment may have been stabilized by microbial mats, aiding preservation.

Many uncertainties about the preservational process remain. What is the meaning of the apparent disappearance of most Ediacaran fossils at the onset of the Cambrian? Fronds similar to *Swartpuntia* from Namibia have been found in Early Cambrian sediments from the Uratanna Formation, South Australia. These fronds occur in association with trace fossils indicative of the Early Cambrian, and demonstrate that the Ediacaran assemblage did not disappear in a mass extinction before the Cambrian, as has been suggested.

Given the phylogenetic quagmire presented by the Ediacaran fossils, the trace fossil record may provide the best potential for interpreting functional aspects, and thus complexity, of Neoproterozoic animals. Many palaeontologists have assumed that the animals that made the trace fossils (burrows and tracks preserved in sediment) were unrelated to the Ediacaran assemblage. On the other hand, the bilateral traces may have been produced by smaller and as yet undescribed Ediacaran fossils (Gehling 1991). The organisms that formed these horizontal to subhorizontal burrows must have had a head of sorts, were bilaterally symmetrical, and

evidently lacked limbs. Determining the diversity of late Neoproterozoic traces is difficult, and may have been seriously overestimated. Most late Neoproterozoic traces are rare, only 1–5 mm in diameter, and vertical burrows are largely lacking; bioturbation of the sediment is essentially unknown (Jensen 1997). Bilateral 'worms' seem to have produced most Neoproterozoic traces, probably with a hydrostatic skeleton. In contrast, trace fossils increase rapidly in diversity, size, and complexity in the Early Cambrian, further confirming the magnitude of the Early Cambrian radiation.

Trace and body fossils have now been augmented by an exciting new source of information about late Neoproterozoic animals. Phosphorites of the Doushantuo Formation (≈580–570 Ma) in southern China preserve, in exquisite three-dimensional detail, early metazoan embryos and a host of algae (Xiao *et al.* 1998). The embryos have undergone several cleavages and include stereoblastulae (a solid ball of cells resulting from early cleavage), indicating the presence of differentiated cell lines and fairly complex development. Since they may be older than all Ediacaran fossils except the discs from the Mackenzie Mountains of Canada, they represent the oldest known metazoan body fossils, but their affinities are unclear. They are probably embryos of cnidarians or bilaterians, and some developmental biologists have argued that they represent protostomes, but they may be embryos of Ediacaran animals. The Doushantuo discovery opens up an extremely promising avenue for future research as it suggests that the early developmental history of metazoans may be directly available to palaeontological inquiry. It also demonstrates that most of the major lineages of algae were present by 570 Ma.

Recent geochronological work has yielded several other important results (Fig. 1.2.1.1). The addition of the lengthy Manykaian Stage to the Early Cambrian, below the Tommotian Stage, came about through the decision to place the base of the Cambrian at the first occurrence of the trace fossil *Treptichnus pedum* in a section in Newfoundland. Thus the recognized Precambrian–Cambrian boundary no longer coincides with the onset of the classic Cambrian radiation at the base of the Tommotian Stage. More importantly, since the redefinition of the boundary, numerous assemblages of small shelly fossils have been found in sediments of Manykaian age in Mongolia (Brasier *et al.* 1996) and Siberia (Knoll *et al.* 1995), extending the small shelly fossils below their original occurrence in the Tommotian (see also Section 1.2.2). The diversity, size, and complexity of trace fossils also increases during the same interval (Jensen 1997). Thus, as more sections are studied in detail, what appeared earlier to be the rapid appearance of these small shelly fossils at the base of the Tommotian sections in Siberia is revealed to be a far more gradual appearance. Finally, the Early Cambrian now accounts for 33 million years of the Cambrian, with only 20 million years for the Middle and Upper Cambrian.

Dating the divergence

When did animals originate? This is not as simple a question as it first appears. When any two groups diverge they will be morphologically similar. With time, accumulated morphological changes distinguish the two lineages. Although the earliest indisputable animal fossils date to 580–560 Ma, the divergence of the metazoan clade from its sister clade must precede this. The critical question is by how much. One approach to the problem is the analysis of slowly evolving gene sequences. It is important to remember, however, the difference between molecular and morphological estimates of divergence dates. Molecular data will allow the timing of divergence of two lineages into distinct species to be estimated, but these species are unlikely to be morphologically distinct. The morphologies which characterize the major clades of animals evolved some time after their divergence. Given the uncertainties of fossil preservation, the earliest organisms with the new morphology are unlikely to be preserved and recovered by palaeontologists. Thus morphological estimates are based on when these distinctive forms appear in the fossil record. The extreme example of this difference is provided by a host of soft-bodied clades which must have diverged from other phyla before the Cambrian radiation, yet are not found in the fossil record.

Molecular estimates of divergence times depend upon a 'molecular clock', based upon the assumption that substitution rates within particular genes are sufficiently regular to allow the branching of two lineages to be dated by comparing molecular sequences (see Section 5.3.6). The clock hypothesis followed from the recognition that many changes in DNA are evolutionarily neutral (and thus not removed by selection). Thus, if the DNA (or, often, RNA) has been sequenced from the same gene in two lineages, and the rates of substitution for the gene can be determined, the date of divergence can be calculated. Many techniques have been developed to test the various assumptions of the molecular clock, and to identify the circumstances in which it can be useful.

But the molecular clock is inherently limited by several factors. First, substitution rates are not regular, and may vary widely between lineages, even for the same gene. For very distant events, such as the metazoan divergence, multiple substitutions have occurred and must be corrected for. Other assumptions must be made about the pattern of rate substitution. Finally, the substitution rates must be calibrated by using a well-dated divergence event from the fossil record. If the calibration event is older than the divergence being estimated with the molecular clock (an interpolated calibration date),

the clock date is more likely to be reliable than if the calibration event is younger (an extrapolated calibration date). This is because dramatic changes in substitution rates, as happen during evolutionary radiations, are more difficult to detect with extrapolated calibrations.

The first attempt at a molecular clock estimate for the divergence of animal phyla dates to 1981, but a more recent, comprehensive analysis (Wray *et al.* 1996) has triggered considerable additional work. A large dataset and more sophisticated analytical techniques lent credence to the results; seven genes were analysed, and a consensus estimate for the divergence of protostomes and deuterostomes was about 1200 Ma, and 1000 Ma for the echinoderm–chordate split. Other workers have attacked the methods used, altered the selection of genes and taxa, and recalibrated the substitution rates. Estimated divergences for the protostome–deuterostome split range between 1500 Ma and 670 Ma!

While all of these results are significantly older than estimates based on the fossil record, their inconsistency is a cause for significant concern. The results do not necessarily require a very early divergence of metazoa. Recall the assumption of rate uniformity inherent in the use of the molecular clock. Greatly increased rates of substitution during evolutionary bursts could also explain the data, for they would violate the assumptions of the clock and make more recent divergences appear older. Recognizing such bursts requires very careful analyses for differences in relative substitution rates between lineages. Such tests have yet to be performed, and thus the reliability of molecular divergence estimates remains uncertain. If, however, the molecular clock estimates are substantially correct and the major metazoan lineages diverged long before the Cambrian radiation, then lineage divergence, and perhaps even the acquisition of some characteristic aspects of particular clades, may have been effectively decoupled from the Cambrian radiation. This in no way reduces the morphological innovations and ecological significance of the radiation. It does, however, strengthen arguments that a change in the physical or biological environment was responsible for the correlated radiation of so many lineages, from unicellular acritarchs to metazoa.

Branches of the tree

Important advances in understanding the relationships between the major clades of animals have been made in the past decade, spurred by a wealth of new molecular data, detailed morphological and ultrastructural studies, and input from comparative molecular developmental biology. Further, the application of rigorous methods of phylogenetic analysis has provided a standard framework for analysing and comparing datasets. While metazoan phylogeny is far from resolved, the field has been revolutionized since the release of the first robust molecular results in 1988.

A consensus metazoan phylogeny from about 10 years ago is shown in Fig. 1.2.1.2(a), and a synthesis of recent

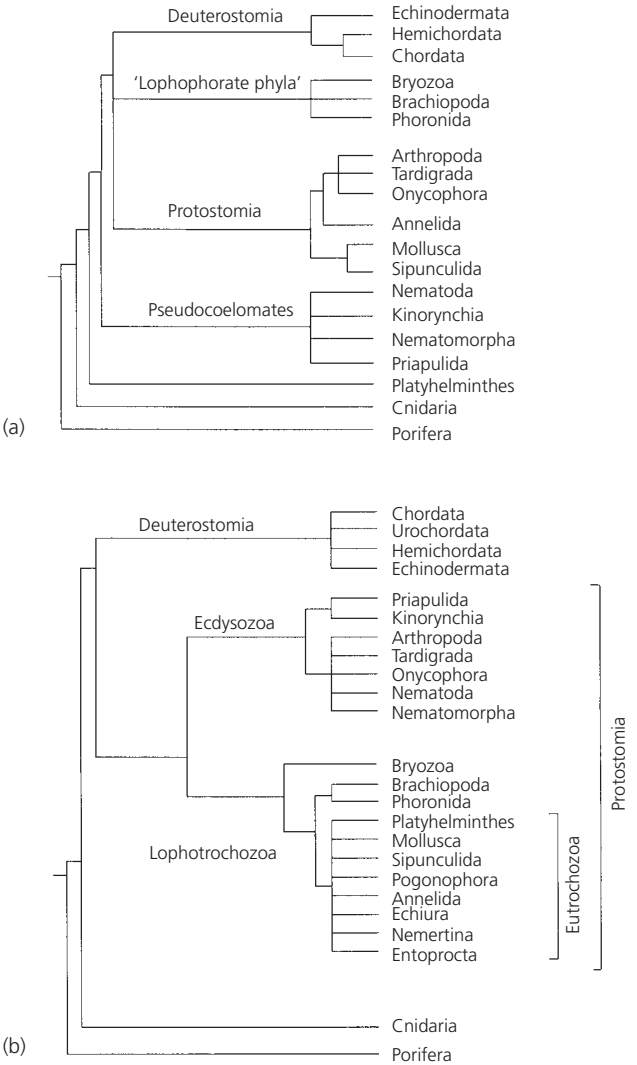


Fig. 1.2.1.2 (a) Consensus metazoan phylogeny before the introduction of recent molecular data and new methods of analysis. The pseudocoelomate phyla diverge before the protostome–deuterostome split, the lophophorate phyla are neither protostomes nor deuterostomes, and arthropods are shown as being more closely related to annelids than molluscs. This figure represents a common American view of metazoan phylogeny; other very different phylogenies were common elsewhere, particularly in Europe, but all differ from (b). (b) Metazoan phylogeny, based on recent analyses of 18S ribosomal DNA, and supported by a variety of developmental data. The pseudocoelomate phyla lie within the protostomes, and the protostomes are divided into two large clades, the Ecdysozoa and Lophotrochozoa. Arthropods are related to a variety of other moulting animals, but are not closely related to either molluscs or annelids. (Based on Aguinaldo *et al.* 1997 and references therein.)

results from 18S ribosomal (r)DNA in Fig. 1.2.1.2(b) (Aguinaldo *et al.* 1997). Several differences are apparent. The clades previously known as the pseudocoelomates, a variety of groups with very simple morphology, have vanished from their position between the cnidarians and the protostome–deuterostome split. Most, if not all, of these groups have greater affinities to protostome clades than to each other. The platyhelminthes (flatworms), a very simple group of worms lacking an anus, may, however, be polyphyletic. The traditional placement of them as a sister group to all higher metazoans may be partly correct, while other flatworms belong within the protostomes (Fig. 1.2.1.2b). The lophophorates (brachiopods, phoronids, and bryozoans) are no longer a jumble of protostome and deuterostome features, but lie at the base of the new clade Lophotrochozoa, one of two major clades within the protostomes. For years invertebrate biologists have debated whether arthropods were more closely related to annelids or molluscs. New moecular data, supported by some developmental inforlmation, suggests that the arthropods are part of the other major basal protostome clade, a group of moulting animals, the Ecdysozoa.

This new topology is likely to be modified as research continues. The data from 18S rDNA analyses may be biased by the particular taxa sampled, uncertainties in aligning the sequences for comparison, and differences in the rates of substitution. It is unlikely that any single gene will ever provide a highly robust phylogenetic framework. New sources of phylogenetic information include other highly conserved nuclear genes, data from gene order and rearrangement, and gene duplications. If the topology shown in Fig. 1.2.1.2(b) is largely correct, a very different evolutionary history is suggested than in Fig. 1.2.1.2(a). A number of features previously considered to have evolved only once, including the coelom and segmentation, clearly evolved multiple times. The steady increase in morphological complexity inherent in Fig. 1.2.1.2(a) has been replaced in Fig. 1.2.1.2(b) by a scenario in which numerous lineages have evidently undergone considerable morphological simplification. Evaluating the relationships of many groups within the Ecdysozoa and Lophotrochozoa continues to be difficult, probably reflecting slow rates of molecular change relative to those of morphological divergence. It is unlikely that genes changed rapidly during an evolutionary radiation and then slowed down to preserve the pattern of change. Resolution of these internal nodes is likely to come from a combination of molecular, developmental, and ultrastructural data.

Developmental innovations

Although the morphologies of nematode worms, flies, and mice seem to have little in common, developmental biologists have recently discovered deep similarities in the genes that control development in these three groups (see Section 2.2.1). The genes controlling the formation of eyes, limbs, the heart, the head, and segmentation are shared between all protostomes and deuterostomes. Thus, these genes, if not necessarily their specific functions, must have been present in their common ancestor. This discovery was entirely unexpected, and the depth of the developmental similarities between different body plans remains unclear. Although the genetic pathways for limb formation, for example, are shared by mice and flies, this does not necessarily mean that these genes produced limbs in the last common ancestor. The genes may have been used for a related purpose and co-opted independently in each lineage. Although this seems unlikely, similar cases are known. Thus when genes are conserved (sequence similarity) this does not necessarily imply that they have the same function. Conversely, even if related genes do have the same function, it may not necessarily have been preserved from the common ancestor of the two lineages (Valentine *et al.* 1999).

In those cases where function has been preserved, developmental information provides a means of reconstructing much of the development and morphology of lineages that diverged during the Cambrian radiation. This opens up another new avenue for understanding the early evolution of animals and reveals that developmental biologists and palaeontologists have both been approaching the same question from different perspectives.

References

Aguinaldo, A.M.A., Turbeville, J.M., Linford, L.S., Rivera, M.C., Garey, J.R., Raff, R.A. and Lake, J.A. (1997) Evidence for a clade of nematodes, arthropods and other moulting animals. *Nature* **387**, 489–493.

Brasier, M.D., Shields, G., Kuleshov, V.N. and Zheballos, E.A. (1996) Integrated chemo- and biostratigraphic calibration of early animal evolution: Neoproterozoic–early Cambrian of southwest Mongolia. *Geological Magazine* **133**, 445–485.

Fedonkin, M.A. and Waggoner, B.M. (1997) The late Precambrian fossil *Kimberella* is a mollusc-like bilaterian organism. *Nature* **388**, 868–871.

Gehling, J.G. (1991) The case for Ediacaran fossil roots to the Metazoan tree. *Memoirs of the Geological Society of India* **20**, 181–223.

Grotzinger, J.P., Bowring, S.A., Saylor, B.Z. and Kaufman, A.J. (1995) Biostratigraphic and geochronologic constraints on early animal evolution. *Science* **270**, 598–604.

Jensen, S. (1997) Trace fossils from the Lower Cambrian Mickwitzia sandstone, south-central Sweden. *Fossils and Strata* **42**, 1–111.

Kaufman, A.J., Knoll, A.H. and Narbonne, G.M. (1997) Isotopes, ice ages and terminal Proterozoic earth history. *Proceedings of the National Academy of Sciences, USA* **94**, 6600–6605.

Knoll, A.H., Kaufman, A.J., Semikatov, M.A., Grotzinger, J.P. and Adams, W. (1995) Sizing up the sub-Tommotian unconformity in Siberia. *Geology* **23**, 1139–1143.

Narbonne, G.M., Kaufman, A.J. and Knoll, A.H. (1994) Integrated chemostratigraphy and biostratigraphy of the Windermere Supergroup, northwestern Canada: implications for Neoproterozoic correlations and the early evolution of animals. *Bulletin of the Geological Society of America* **106**, 1281–1292.

Narbonne, G.M., Saylor, B.Z. and Grotzinger, J.P. (1997) The youngest Ediacaran fossils from southern Africa. *Journal of Paleontology* **71**, 953–967.

Seilacher, A. (1992) Vendobionta and Psammocorallia: lost constructions of Precambrian evolution. *Journal of the Geological Society of London* **149**, 607–613.

Sun, W.G. (1994) Early multicellular fossils. In: S. Bengston, ed. *Early life on Earth*, pp. 358–369. Columbia University Press, New York.

Valentine, J.W., Jablonski, D. and Erwin, D.H. (1999) Fossils, molecules and embryos: new perspectives on the Cambrian explosion. *Development* **5**, 851–859.

Wray, G.A., Levinton, J.S. and Shapiro, L.H. (1996) Molecular evidence for deep Precambrian divergences among metazoan phyla. *Science* **274**, 568–573.

Xiao, S.H., Zhang, Y. and Knoll, A.H. (1998) Three-dimensional preservation of algae and animal embryos in a Neoproterozoic phosphorite. *Nature* **391**, 553–558.

1.2.2 Significance of Early Shells

S. CONWAY MORRIS

Introduction

The crack of the skier's leg or the smashing open by the thrush of a snail's shell epitomize our sense of the skeleton: integral to the organism, of obvious functional significance, yet potentially vulnerable. To the palaeontologist they represent our principal source of evidence. Yet many animals are soft-bodied (or with skeletons so delicate as to have a minimal preservation potential), while amongst 'robust' skeletons there is a wide spectrum of resistance against postmortem destruction. Prior to about 550 Ma fossil skeletons are almost entirely absent, at least in the familiar manifestation of shells, conchs, carapaces, spicules, and sclerites. Whether or not the Cambrian 'explosion' is a 'real' evolutionary event, as against a breaching of taphonomic thresholds that ended a protracted and cryptic history of animal evolution, remains controversial. Nevertheless, the diversity of skeletons does take a quantum leap at the beginning of the Cambrian.

In the oldest generally accepted mineralized animal skeletons, those of the Ediacaran-age (Fig. 1.2.2.1) taxon *Cloudina* (Fig. 1.2.2.2), there is evidence for a high organic content that gave the tube wall flexibility. *Cloudina* itself has received considerable attention (Grant 1990), but only recently have other biomineralized taxa been recognized (see Grotzinger *et al.* 1995). All these fossils, mostly simple tubes, occur in carbonates and the role of clastic sediments as a potential source of information is yet to be evaluated. So too do the even earlier stages of biomineralization, of which there is no effective record. Most probably the initial degree of mineralization was very light: one might conceive, for example, of isolated calcareous granules embedded in an organic matrix.

In the Lower Cambrian there was a pronounced episode of sedimentary phosphatization, a by-product of which was, in selected areas and horizons, widespread replacement of calcareous skeletons by diagenetic phosphates. It is clear, however, that there is a bias towards the preservation of smaller fossils, probably because of a preference for the processes of phosphatization to occur in microcavities. For example, there is an abundance of phosphatized molluscs and other cap-like forms of millimetric size. These fossils are readily released by digestion of carbonates in weak acid. The ease of this method means that 'crack-out' collection from comparable sediments is less popular, but significantly it reveals order-of-magnitude larger fossils. Similarly, minute sclerites are often favoured as sites of diagenetic phosphatization, even though the original animals with a scleritome composed of several thousand sclerites were much larger. In those skeletons with a high organic content, as inferred from crumpling and other distortion (Fig. 1.2.2.3a), phosphatic replacement ensures survival in fossils that otherwise would probably have a low preservation potential. Many of the Lower Cambrian groups with primary phosphatic skeletons are either of enigmatic phyletic status, such as mobergellans (Fig. 1.2.2.3b) and tommotiids (Fig. 1.2.2.3c), or belong to groups such as hadimopanellids (Fig. 1.2.2.3d) and protoconodonts whose modern representatives (i.e. priapulids and chaetognaths, respectively) show no comparable biomineralization. In this sense, there has been a subsequent shift in utilization of phosphate to the vertebrates.

Metazoan phylogeny

Although it is a palaeontological truism that skeletons appear abruptly at the beginning of the Cambrian, a number of staging posts can be identified. For example, while not unequivocally confirmed, it is likely that *Cloudina* (Fig. 1.2.2.2) is effectively confined to Ediacaran-age strata. In contrast, echinoderms appear not to make a debut until the middle Atdabanian. Precise U/Pb zircon dates place the age of the Vendian–Cambrian boundary at ≈ 550 Ma, but the timing of the stratigraphic slices that define correlatable units of the

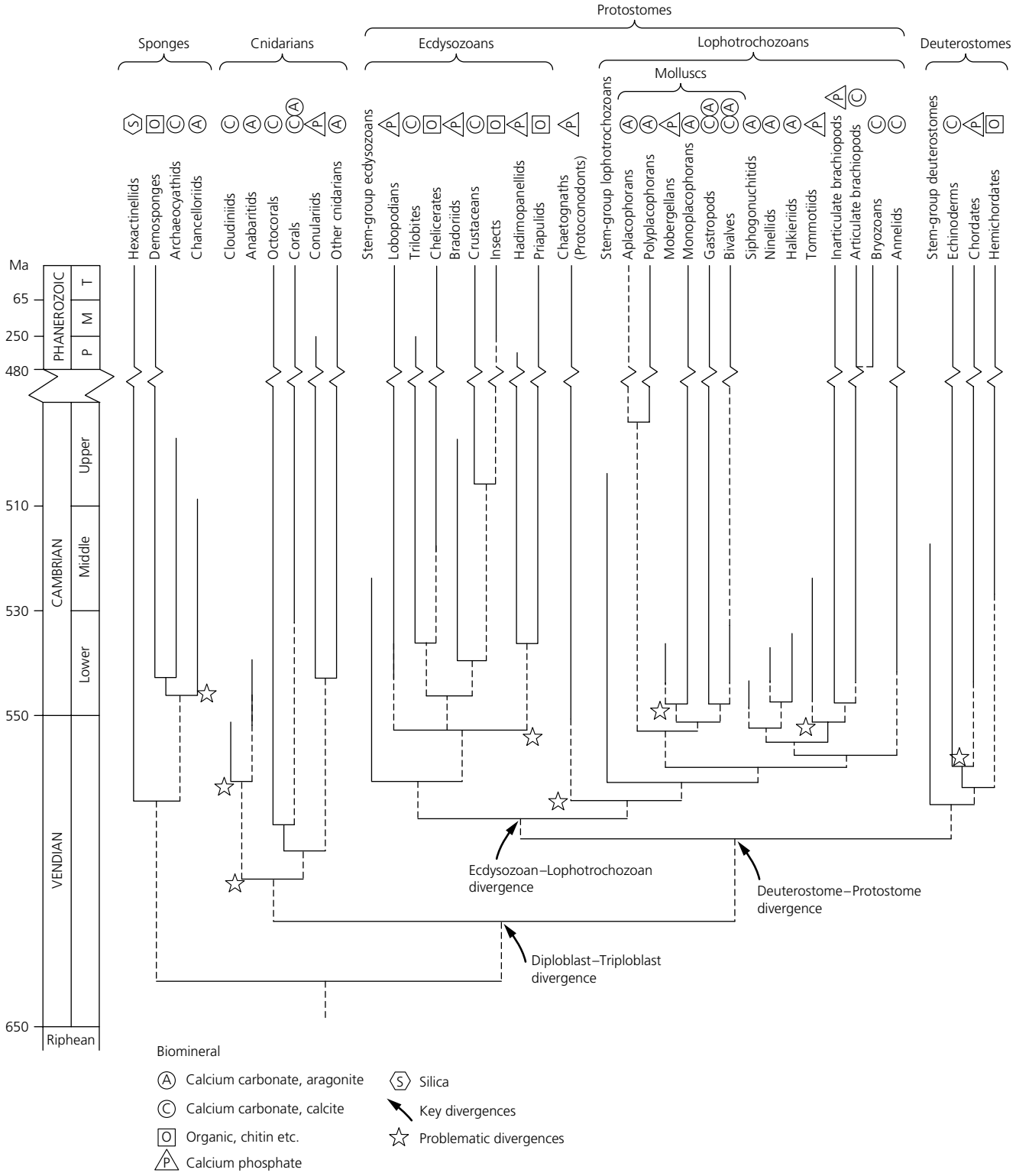


Fig. 1.2.2.1 Outline phylogeny of the Metazoa, emphasizing the distribution of biominerals. Only the principal biominerals are indicated, and subsidiary occurrences such as calcium sulphate in the statoconia of scyphozoans or ferric phosphate in holothurians (see Lowenstam and Weiner 1989) are not included. Many aspects of this phylogeny, which is based on multiple lines of evidence from anatomy, palaeontology, and molecular biology, remain controversial. The divergences that are especially questionable are indicated with a star. Inferred, or ghost, ranges are depicted with dashed lines, but the exact geological ages of the divergences are only indicative.

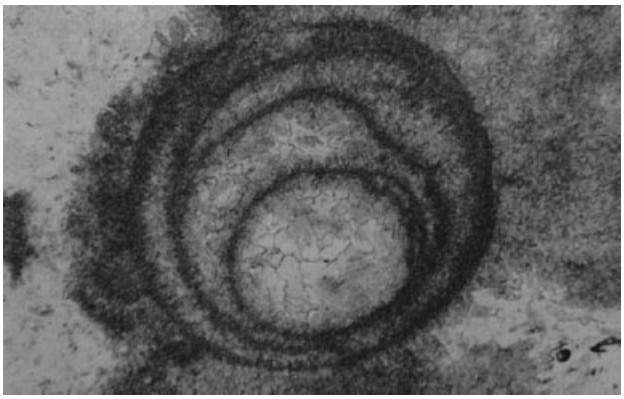
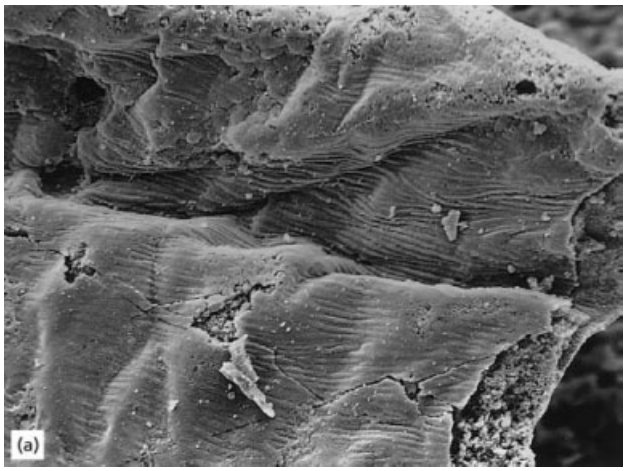
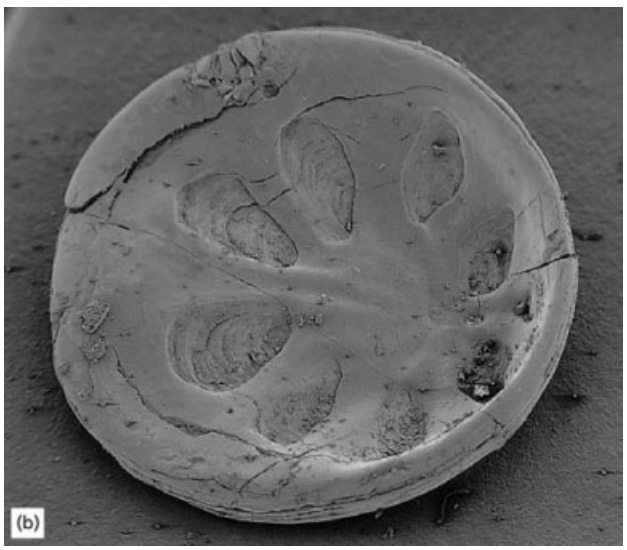
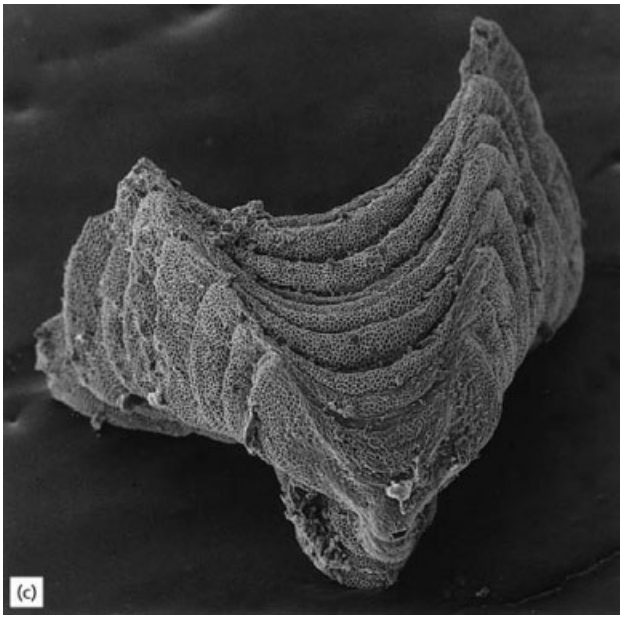


Fig. 1.2.2.2 *Cloudina*, transverse section of tube, subsurface Ediacaran, Ara Formation, Oman, ×32. (Reproduced with permission from Conway Morris, S., Mattes, B.W. and Chen, M. (1990) *Am. J. Sci.* **290A,** 245–260; Fig. 4.16.)







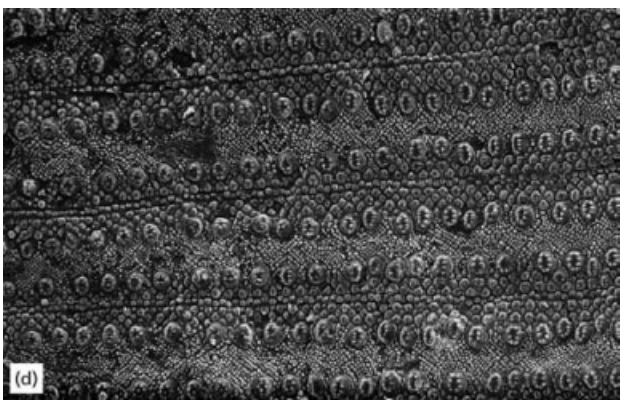


Fig. 1.2.2.3 (a) Detail of surface of the conulariid (carinachitid) *Carinachites*, to show folding of originally organic-rich skeleton, Lower Cambrian, Hongchunping Formation, Shaanxi, China, ×540. (Reproduced with permission from Conway Morris, S. and Chen, M. (1992) *J. Paleont.* **66,** 384–406; Fig. 9.15.) (b) The mobergellan *Discinella*, in ventral view to show the prominent muscle scars, Lower Cambrian, New York, ×22. (Reproduced with permission from Conway Morris, S. and Chapman, A.J. (1997) *J. Paleont.* **71,** 968–985; Fig. 10.1.) (c) The tommotiid *Paterimitra*, isolated sclerite, Lower Cambrian, Ajax Limestone, South Australia, ×112. (Reproduced with permission from Bengtson, S., Conway Morris, S., Cooper, B.J., Jell, P.A. and Runnegar, B.N. (1990) *Mem. Ass. aust. Palaeont.* **9,** 1–364; Fig. 92B.) (d) Latex cast of articulated array of hadimopanellid sclerites from *Palaeoscolex*, Lower Ordovician, Shineton Shale, England, ×225. (Reproduced with permission from Conway Morris, S. (1997) *Zool. J. Linn. Soc.* **119,** 69–82; Fig. 1.)

Vendian and Cambrian are less constrained. So too is the actual precision of stratigraphic correlations, although on the basis of chemostratigraphy sponge spicules from Mongolia appear to be of Ediacaran-equivalent age (Brasier *et al.* 1997), a discovery concordant with similar-aged soft-bodied fossils of sponges (Gehling and Rigby 1996). The principal episode of animal biomineralization occupied an interval of about 20 million years as presently dated (530–550 Ma). Nor was this the final word in skeletal development. Subsequently some groups appear to have lost the ability to mineralize. For example, in the halkieriid–wiwaxiid clade (Conway Morris and Peel 1995) the former group had robust calcareous (probably aragonitic) sclerites, whereas in the wiwaxiids the sclerite wall was organic. Even though a consensus on metazoan phylogeny is not available, it is unlikely that any configuration (Fig. 1.2.2.1) would conclude that biomineralization was monophyletic. The range of biominerals involved, notably silica, calcium carbonate (as both aragonite and calcite), and phosphate, also points to polyphyly (Fig. 1.2.2.1). Little is known about how the organic templates initiate and control crystal growth. It is at least clear that glycoproteins and acidic proteins (rich in aspartic acid) are important (Addadi and Weiner 1985), but so in some circumstances may be phospholipids and glycosaminoglycans. The recognition that different proteins control aragonite and calcite precipitation in the same animal (Belcher *et al.* 1996) can be contrasted, for example, with surprising evidence from diatoms (Kröger *et al.* 1994) which indicates that the structural protein involved with silica precipitation may be employed in other groups to form carbonate biominerals. Even less is known about the genes for biomineralization, but so far as our understanding of molecular evolution goes we might predict that genes and their protein products are co-opted on a multiple basis. It will not be surprising if the requirements for template construction lead to convergence and that unrelated genes are drawn upon for the necessary deployment.

Extrinsic and intrinsic factors

Implicit in this view, and inherent in any scheme of metazoan phylogeny (Fig. 1.2.2.1), is that not only is biomineralization polyphyletic but it is also opportunistic. It has been argued that such an opportunity could only arise, or at least be facilitated, as a response to changing ocean chemistry. This finds a direct resonance with the proposed correlation between an abundance of sedimentary phosphates, the inference of elevated phosphorus levels in sea water, and a supposed excess of phosphatic skeletons in contrast to the remainder of the Phanerozoic. The last item, however, finds little support from the fossil record. Nevertheless, in the case of calcium carbonate, and specifically the polymorphs calcite and aragonite, there is some evidence of a correlation with seawater chemistry (Harper *et al.* 1997). What would be less likely, at least in the case of animals, is that changes in seawater chemistry actually initiated the Cambrian 'explosion' of biomineralization.

It seems more probable that the primary motor for the widespread appearance of skeletons was ecological, and of paramount importance was protection against predatory attack. There is little evidence that early predators enjoyed the benefits of beweaponed biomineralization. Apart from the phosphatic teeth of the chaetognathous protoconodonts, such evidence as we presently have (principally from Burgess Shale-type faunas; Conway Morris 1998) is that prey last saw the light of day in the gullets of priapulids as well as the limbs and jaws of arthropods, none of which was actually mineralized. Direct evidence for predation is relatively limited and includes gut contents, boreholes, and coprolites. The arrangement of skeletons is, however, suggestive. These include the cataphract skeletons, most notably of the halkieriids, which combine flexibility and protection. Many other Cambrian fossils are cap-like or bivalved, and would have given some protection against durophagy. So too would the spicular arrangement of the sponges, chancelloriids, and octocorals. This is not to deny other functions to skeletons. The argument for support and muscle insertion has some force, yet most animals lacking mineralized skeletons still remained functionally uncompromised.

Skeleton space

There are perhaps two approaches to classifying these early skeletons. One is to consider which Cambrian groups possess biominerals, what is their composition and microstructure, and what range of functions they encompass. The second approach is more synthetic, and makes no necessary reference to phylogeny. One such (Thomas and Reif 1993) is based on a code of skeletal types, e.g. rigid, cones, imbricate, and their combinatorial associations (Fig. 1.2.2.4). In this way a matrix of occurrences can be completed, with the further discrimination of relative frequencies. Almost every skeletal variation has been tried and, more significantly, in many cases the 'invention' of a particular arrangement is blatantly polyphyletic (Fig. 1.2.2.4a). It is also possible to begin to investigate how this matrix was filled during the Vendian–Cambrian diversifications. So far as the Vendian is concerned, very few types are readily identifiable, notably tubes of *Cloudina* (Fig. 1.2.2.2) and sponge spicules. The succeeding basal interval of the Cambrian (Nemakit–Daldyn or Manykay Stage) is also skeletally depauperate, with mostly tubes, shell-like taxa, and protoconodont teeth. Thereafter, however, the

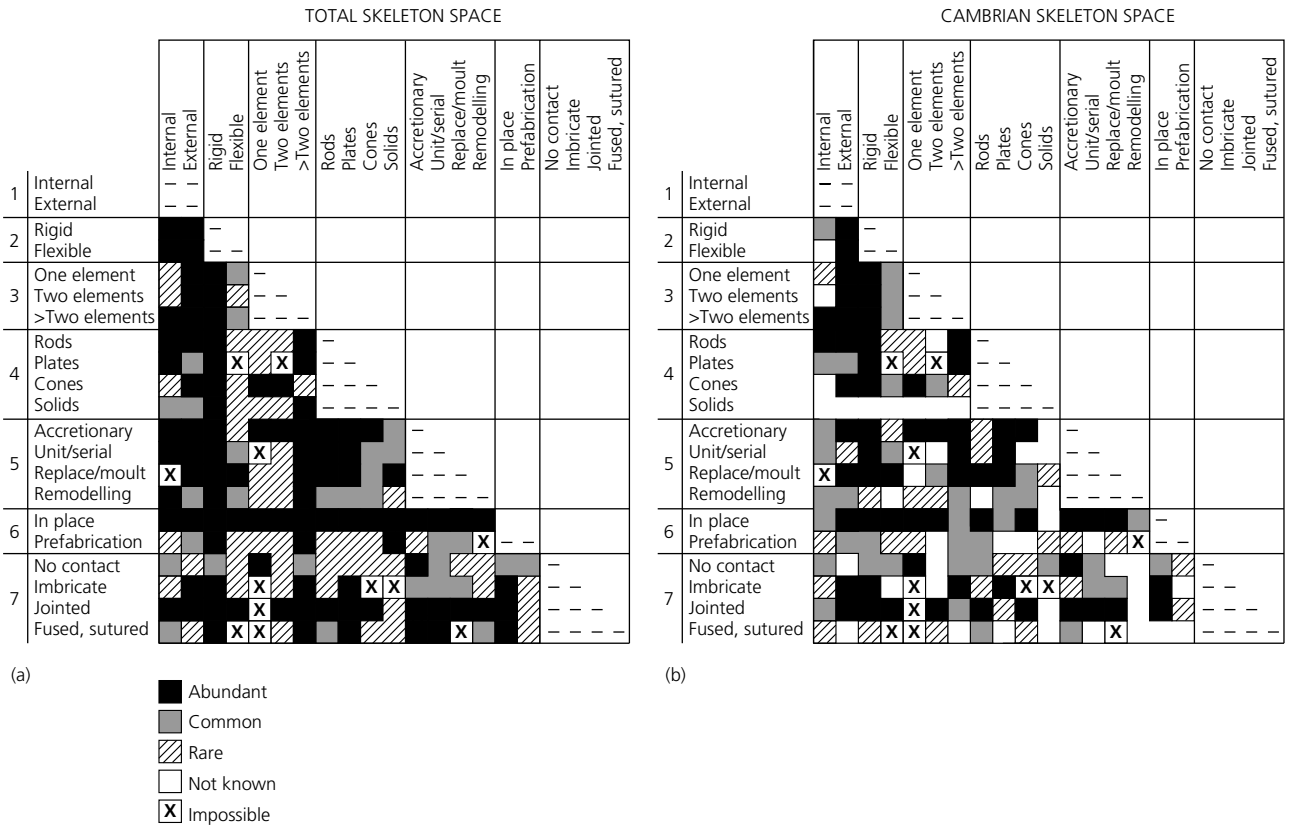


Fig. 1.2.2.4 A depiction of 'skeleton space' whereby a matrix is defined by 21 variables, divided into seven categories, which together define 186 possible pairs of character combinations. Of these a few are functionally impossible, a few others are potentially possible but have not been recognized, and the remainder are variably abundant (rare, common, abundant). (a) Total skeleton space. (Redrawn from Fig. 12 of Thomas and Reif 1993.) (b) Cambrian skeleton space. (Data based on Thomas, R.D.K. and Reif, W.-E. (1991) In: N. Schmidt-Kittler and K. Vogel (eds). *Constructional morphology and evolution*, pp. 283–294.)

'barrel' of skeleton design fills quickly, and Fig. 1.2.2.4(b) attempts to show the situation by the end of the Middle Cambrian. Comparing the two matrices (Fig. 1.2.2.4a,b) it is evident that the post-Cambrian expansion into the known totality of skeleton space was relatively modest, and was most notable in the category of 'solids', i.e. structures such as vertebrate teeth/bones and belemnites.

Taxonomic distribution

In terms of this heading it is convenient to divide the topic into two somewhat artificial sections, relating, respectively, to those groups which are taxonomically 'uncontroversial' vs. those that are more enigmatic. The ultimate aim is to accommodate all these data into a coherent scheme of metazoan phylogeny (Fig. 1.2.2.1). Readers of the future may wish to compare the entries between this *Palaeobiology II* and, say, *Palaeobiology VII* !

By general consensus the most primitive metazoans are sponges. Siliceous spicules of presumed hexactinellids have been identified from Ediacaran-age strata of Mongolia (Brasier *et al.* 1997) and south-central China. The Cambrian record of sponge spicules is more complete, and articulated arrays are well known from Burgess Shale-type faunas. Sponges were also the first major group to form massive calcareous skeletons. These are the archaeocyathids, some of which formed highly integrated skeletons related to an aquiferous system. Much more controversial are the chancelloriids, known from rosettes of hollow sclerites whose growth pattern resembles that of the sachitids and the halkieriids (see below). The chancelloriid body, however, was sponge-like, consisting of a bag-like structure attached to the sea floor with the rosettes scattered over the integument.

The Ediacaran–Cambrian record of cnidarians is rather less satisfactory. The tubes of *Cloudina* (Fig. 1.2.2.2) were conceivably inhabited by some sort of polyp. Structures identified as spicules are also claimed to occur in the Ediacaran frond-like fossils, such as *Charniodiscus*,

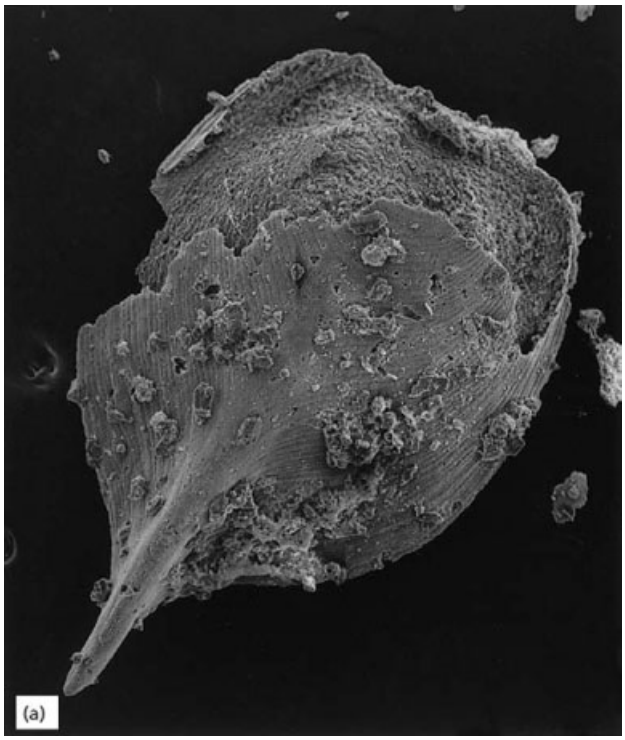
whose position as pennatulacean anthozoans seems moderately secure. Nevertheless, the presumed pennatulacean *Thaumaptilon*, from the Middle Cambrian Burgess Shale (Conway Morris 1998), lacks evidence for spicules. In contrast isolated octocoral spicules have been identified with some confidence in the Cambrian. The Cambrian record of corals is unsatisfactory, but putative examples of rugosans and tabulates are recorded. Convincing examples of early conulariids (Fig. 1.2.2.3a) suggest a connection to the scyphozoans, specifically the chitinous tube which in some living taxa houses the polyp which buds in a process known as strobilation. The Cambrian examples, referred to as carinachitids and hexanguloconulariids, appear to have been composed of phosphate minerals, albeit with a liberal addition of organic matter. Their overall form and especially the pronounced tetraradial symmetry are consistent with a cnidarian relationship. What may be a related form is known as *Punctatus*, and this provides a series of remarkable insights into Cambrian ontogeny because it is possible to trace its development, which is direct, from a prehatched embryo to an adult tube (Bengtson and Yue 1997).

In the Cambrian a variety of protostome phyla are well represented in the skeletal assemblages. These include the familiar arthropods, especially trilobites and bradoriids, the brachiopods (inarticulate and articulate), and molluscs. The last group is dominated by cap-shaped fossils, ostensibly monoplacophorans. Also identified in Early Cambrian assemblages are gastropods, rostroconchs, and bivalves. Cephalopods and chitons do not appear in the fossil record until the Upper Cambrian. The monoplacophorans are diverse, but their phylogeny is controversial (Peel 1991). Problems of analysis are compounded by a welter of cap-like objects, of which only a few ultimately may prove relevant to understanding the early evolution of molluscs. Whether or not the first molluscs were segmented, on which hangs a potentially key role for the chitons and certain aplacophorans, has been extensively but inconclusively debated. Skeletal remains, by themselves, are unlikely to resolve this issue.

Brachiopods are conspicuous in Cambrian assemblages, but here too the story is far from simple. Inarticulates probably predate articulates stratigraphically, but their interrelationships are obscure. Some inarticulate groups, notably the kutorginiids and mickwitziids, have unusual morphologies. The former have been identified, tentatively, as intermediates between the inarticulates and articulates. Mickwitziids are notable for their large shell size and complex microstructures: are they actually brachiopods? Other groups are yet more enigmatic. Helpfully labelled the 'pseudobrachiopods', this group of apparently bivalved shells are best known from South Australia, but also have representatives in China. The valves are deeply convex, have protuberances and corresponding recesses suitable for articulation, and areas for muscle insertion. Nevertheless, the best-known taxon *Apistoconcha siphonalis* (Fig. 1.2.2.5a) is peculiar in having margins between the opposing valves that are far from congruent. One suggestion is that the 'gaps' were filled with smaller plates; another possibility looks towards a halkieriid-like model (see below).

The arthropod record is dominated by the calcareous skeletons of trilobites. In certain groups, such as the burlingiids, the exoskeleton is conspicuously thin, whilst in the related naraoiids there is no mineralization. Amongst the bradoriids, which have traditionally been placed amongst the ostracods but are now regarded as a distinctive group, some taxa have phosphatic valves. As with any group discussed here a coherent discussion of biomineralization can only be achieved in the context of an agreed phylogeny (Fig. 1.2.2.1). For arthropods morphological character analysis has provided a series of cladograms. These, however, show various discrepancies with data from molecular biology, which in turn throw doubt on the phylogenetic reality of such concepts as the Atelocerata (= myriapods + insects). It is also clear from the Burgess Shale-type faunas (Conway Morris 1998) that the great majority of arthropods lacked cuticular mineralization. Moreover, in the stem-group lobopodians the bosses and spines that characterize the 'armoured' varieties are either heavily cuticularized (e.g. *Hallucigenia*) or, in the case of *Microdictyon*, are composed of a reticulate disc of phosphate. Whilst a defensive role for this structure is generally agreed, the reasons for phosphatic biomineralization in *Microdictyon* are not known.

Amongst the deuterostomes there are only mineralized remains of echinoderms, although the organic tubes of hemichordates are also recognized. The unique structure of the stereom skeleton of echinoderms permits easy identification of isolated ossicles. Rarer examples of articulated material, typically preserved in obrution deposits, reveals a bewildering array of groups, including 'eocrinoids', helicoplacoids, solutans, cinctans and ctenocystoids. The origin of the stereom tissue is obscure, but one might speculate that it was preceded by a mesodermal zone of collagenous fibrils that acted as a template. In the Burgess Shale animal *Echmatocrinus*, which has been interpreted as a primitive crinoid, the thin plates that coat the surface would be interpreted as a reduced stereom. An alternative proposal, however, places *Echmatocrinus* in the anthozoan cnidarians. The early phylogeny of chordates remains very controversial. Unequivocal chordate biominerals do not occur until the Middle Cambrian if, that is, the phosphatic elements of the paraconodonts (Müller and Hinz-Schallreuter 1998) are correctly identified as the teeth-like precursors of those seen in the euconodonts, or if the fragmentary remains of the Upper Cambrian *Anatolepis* are accepted as the earliest fish scales.



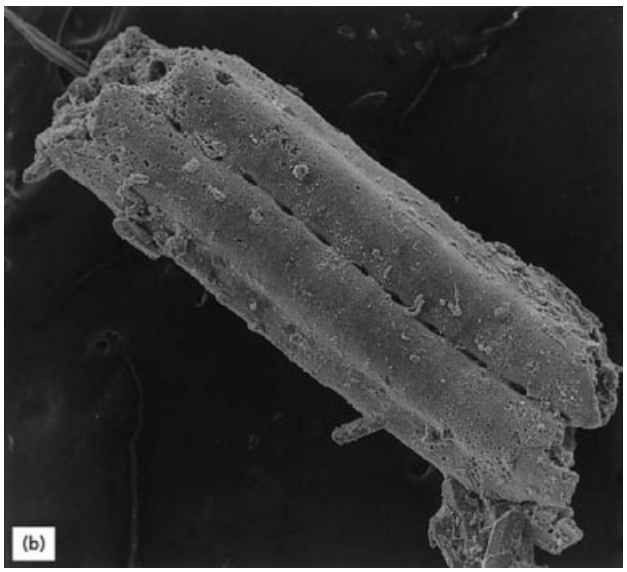


Fig. 1.2.2.5 (a) The so-called 'pseudobrachiopod' *Apistoconcha*, preserved by diagenetic phosphatization that has coated the exterior shell with its growth lines and also provided an internal mould that preserves details of articulation and muscle insertion, ×70. (b) The tube *Anabarites*, defined by a triradial or hexaradial symmetry; the latter is the case here, hence the specific name *sexalox*, ×80. (c) An isolated halkieriid sclerite of *Thambetolepis*, belonging to the category of cultrate and in life inserted on the lateral region of the body, ×100. (Reproduced with permission from Bengtson, S., Conway Morris, S., Cooper, B.J., Jell, P.A. and Runnegar, B.N. (1990) *Mem. Ass. aust. Palaeont.* **9,** 1–364; Figs 110E, 128A, 53A, respectively.)

Enigmatic taxa

Early Cambrian skeletal faunas are well known for their large number of enigmatic taxa, and many Cambrian taxa remain refractory to analysis. This area is best considered in terms of two categories: tubes and scleritomes. The former are a conspicuous component of many Early Cambrian assemblages. Some are simple and are composed either of calcium carbonate (e.g. coleolids), or phosphatic minerals (e.g. hyolithellids). It is likely that they were built by an annelidan-grade organism, but no direct proof is available. Tubes with three- or six-fold symmetries are known as anabaritids (Fig. 1.2.2.5b). A tenuous link has been proposed between the anabaritids and various Ediacaran fossils, most notably *Tribrachidium*, which also display a three-fold symmetry and may be cnidarian (Fig. 1.2.2.1).

In none of these cases is there unequivocal evidence for an operculum, although a possible instance in an anabaritid from central China is on record. Amongst the various proposals for the function of the phosphatic mobergellans (Fig. 1.2.2.3b), that of an operculum

receives some support. The interior displays prominent muscle scars arranged about a plane of bilateral symmetry. Their microstructure varies, and in a species from south-west Mongolia the equivalent structures consist of a plaque containing an array of radiating fibres. The hypothesis that mobergellans represent an operculum suffers some problems in as much as corresponding tubes have not been recognized. One possibility is that, for some reason, the tube was much more lightly mineralized than the phosphatic disc. An alternative is that mobergellans were either univalved, in a manner reminiscent of monoplacophorans, or even bivalved.

The importance of scleritomes in the Cambrian has become increasingly clear in recent years. Two notable breakthroughs concern the halkieriids (Fig. 1.2.2.5c) and the hadimopanellids. Prior to the discovery of *Halkieria evangelista* from the Sirius Passet Lagerstätte in North Greenland (Conway Morris and Peel 1995), reconstructions of halkieriids largely relied on comparisons with articulated material of *Wiwaxia corrugata*. The Greenland material demonstrates a slug-like animal with a sclerite-ome composed of 2000 sclerites and, more surprisingly, a prominent shell at either end of the body. This cataphract arrangement is consistent with a protective role, while the shells in addition may have acted, respectively, as a platform for muscle insertions (anterior) and a covering for a respiratory chamber possibly housing ctenidia (posterior). The biomineral employed was probably aragonite, but there is a clear dichotomy of secretory styles in *Halkieria* between the interpolation of sclerites, which remain at a fixed size, as against growth along an accretionary margin in either shell. Halkieriid sclerites had already been widely recognized as isolated fossils, but the recognition of the *in situ* shells has promoted a reconsideration of various cap-like shells, isolated in acid-etched residues, as possibly being derived from halkieriid-like skeletons.

The clear similarities between siphogonuchitid and ninellid (Fig. 1.2.2.1) (and perhaps sachitid) sclerites and those of halkieriids also invites application of a sclerite-ome model. In the case of the siphogonuchitids, the scleritome, which has yet to be recognized in an articulated form, may have been more primitive in having only two main types of sclerite and a shell composed of sclerites embedded in a ground-mass. In the less well-known ninellids, and possibly sachitids (which some workers suggest are related to the chancelloriids), the sclerite complement may have been more uniform. Finally, in some related groups the sclerites may have either been lost or become unmineralized, whereas the terminal shells remained mineralized. Such might apply to *Oikozetes* from the Burgess Shale, and possibly the 'pseudobrachiopods' (Fig. 1.2.2.5a) (Parkhaev 1998), both of which are known from two distinct types of shell.

The halkieriids (and wiwaxids) have also been given a wider significance as potentially occupying a key position in early protostome evolution (Conway Morris and Peel 1995). As well as having a generalized and possibly superficial similarity to the chitons and aplacophorans, widely believed to resemble primitive molluscs, there are more specific similarities to the brachiopods and annelids. The implications for this hypothesis are yet to be explored (or refuted), but whatever the origins of the bivalved brachiopods, the two valves never derived from a single plate which developed a median zone of weakness, as was the case in bivalves and the juliid gastropods, as well as ostracods and other bivalved arthropods. Brachiopods lack a ligament and each valve must have been derived from separate growth centre.

Hadimopanellid sclerites were first recognized in 1977, and in the absence of articulated material speculation on their affinities was virtually unconstrained: even chordates were proffered as a possibility. It was, however, clear that the most probable function was as a dermal armour. Recognition of phosphatized pieces of cuticle, discovery of exceptionally preserved material in Ordovician nodules, and re-examination of the type species of *Palaeoscolex* (*P. piscatorum*) revealed that the sclerites formed a closely packed cuticular array (Fig. 1.2.2.3d). It is now clear that hadimopanellids are effectively synonymous with the palaeoscolecidans (which include the Burgess Shale taxon *Louisella*), and that they are either priapulid worms or very closely related. Living priapulids have complex cuticular structures, but these are unmineralized and seem to have no close similarities to those found in the Cambrian. The diversity of Cambrian priapulids is incompletely surveyed. *Cricocosmia* from the Chengjiang Lagerstätte, in which the trunk bears two rows of prominent boss-like sclerites, is a reminder that other enigmatic skeletal material in the Cambrian may yet find a home in the priapulids.

Concerning other skeletal remains that almost certainly were arranged in a scleritome, the two principal groups are the cambroclaves and tommotiids. The former are calcareous, and small arrays reveal a tightly integrated scleritome (Fig. 1.2.2.6a). A more primitive state may have consisted of a scleritome with nail-like sclerites scattered over an integument. As with a number of other Cambrian groups, the taxonomic limits of the cambroclaves are fuzzy. Most probably the paracarinachitids belong here, but their proposed assignment to the chitons is highly questionable. The wider affinities of the cambroclaves are not known.

The tommotiids, despite being comparatively well understood, still defy a secure phyletic placement. The original mineralogy was phosphatic, and the sclerites show a wide variation of form encompassing taxa such as *Paterimitra* (Fig. 1.2.2.3c), *Eccentrotheca*, *Lapworthella* (Fig. 1.2.2.6b), *Micrina*, *Dailyatia*, *Camenella*, and *Tann-*

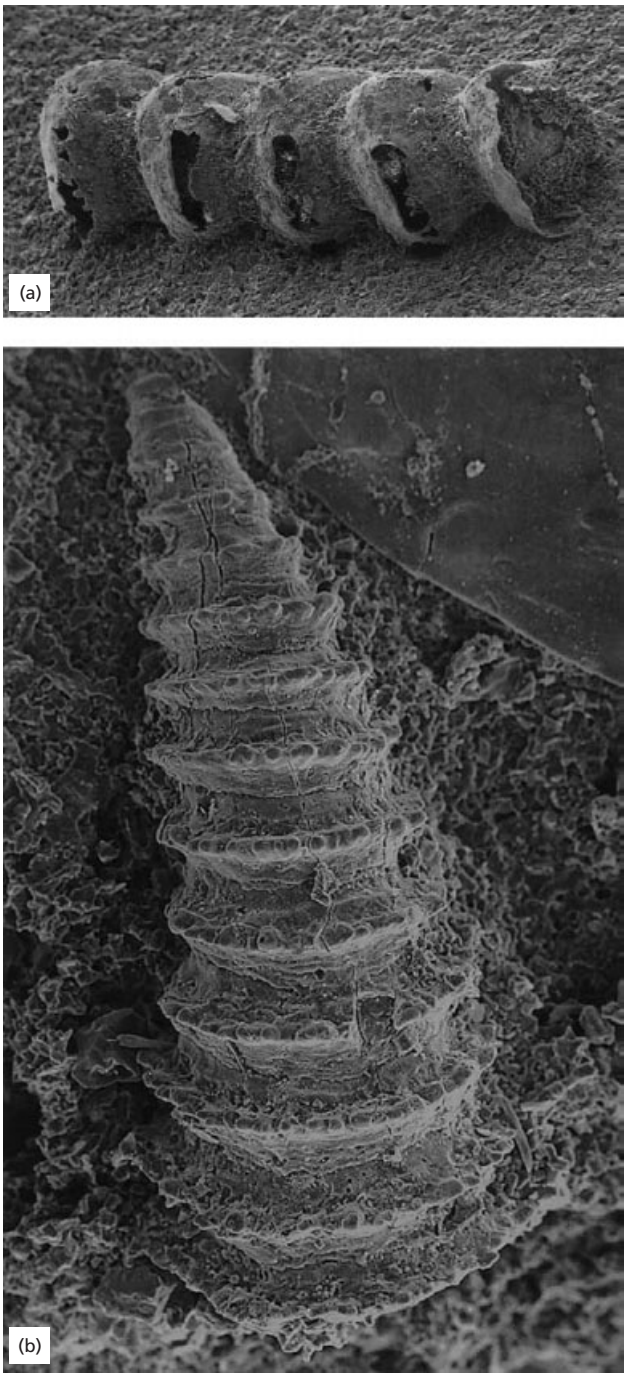


Fig. 1.2.2.6 (a) An articulated array of the cambroclave *Deltaclavus*, Lower Cambrian, Shuijingtuo Formation, Hubei, China, ×100. (Reproduced with permission from Conway Morris, S. and Chen, M. (1991) *Palaeontology* **34,** 357–397; Fig. 9c.) (b) An isolated sclerite of the tommotiid *Lapworthella*, Lower Cambrian, New York, ×270.

uolina. In the last two genera there is evidence of two sclerite morphs, whereas the scleritome of *Dailyatia* was apparently more complex. Left and right morphs point to a bilaterally symmetrical animal. Yet in *Lapworthella* such distinctions are not possible despite well-ordered patterns of sculpture, whilst *Eccentrotheca* can only be described as disorganized (the specific name *guano* was not given lightly). Even more confusingly *Micrina* has what appears to be articulatory teeth, but no counterpart against which to articulate. Tommotiids may, of course, be polyphyletic. Taxa such as *Tannuolina* and *Micrina* bear striking similarities to brachiopods, yet may be convergent. Discovery of the tommotiid scleritome is eagerly awaited.

Future work

Although the skeletal record provides important insights, taken alone it will remain incomplete if not misleading. Exceptional preservation in the form of Burgess Shale-type faunas and early phosphatization (including Orsten assemblages) will provide the main drivers of enquiry. As molecular biology has contributed to the framework of metazoan phylogeny, so too will it underpin our understanding of the processes of biomineralization. In these ways we will not only gain additional insights into the Cambrian 'explosion' but also unravel those evolutionary trajectories that led, ultimately, to the femur of a skier and the shell of a garden snail.

References

Addadi, L. and Weiner, S. (1985) Interactions between acidic proteins and crystals: stereochemical requirements in biomineralization. *Proceedings of the National Academy of Sciences, USA* **82**, 4110–4114.

Belcher, A.M., Wu, X.H., Christensen, R.J., Hansma, P.K., Stucky, G.D. and Morse, D.E. (1996) Control of crystal phase switching and orientation of soluble mollusc-shell proteins. *Nature* **381**, 56–58.

Bengtson, S. and Yue, Z. (1997) Fossilized metazoan embryos from the earliest Cambrian. *Science* **277**, 1645–1648.

Brasier, M., Green, D. and Shields, G. (1997) Ediacaran sponge spicule clusters from southwestern Mongolia and the origins of the Cambrian fauna. *Geology* **25**, 303–306.

Conway Morris, S. (1998) *The crucible of creation: the Burgess Shale and the rise of animals*. Oxford University Press, Oxford.

Conway Morris, S. and Peel, J.S. (1995) Articulated halkieriids from the Lower Cambrian of North Greenland and their role in early protostome evolution. *Philosophical Transactions of the Royal Society of London B* **347**, 305–358.

Gehling, J.G. and Rigby, J.K. (1996) Long expected sponges from the Neoproterozoic Ediacara fauna of South Australia. *Journal of Paleontology* **70**, 185–195.

Grant, S.W.F. (1990) Shell structure and distribution of *Cloudina*, a potential index fossil for the terminal Proterozoic. *American Journal of Science* **290A**, 261–294.

Grotzinger, J.P., Bowring, S.A., Saylor, B.Z. and Kaufman, A.J. (1995) Biostratigraphic and geochronologic constraints on early animal evolution. *Science* **270**, 598–604.
Harper, E.M., Palmer, T.J. and Alphey, J.R. (1997) Evolutionary response by bivalves to changing Phanerozoic sea-water chemistry. *Geological Magazine* **134**, 403–407.
Kröger, N., Bergsdorf, C. and Sumper, M. (1994) A new calcium binding glycoprotein family constitutes a major diatom cell wall component. *EMBO Journal* **13**, 4676–4683.
Lowenstam, H.A. and Weiner, S. (1989) *On biomineralization*. Oxford University Press, New York.
Müller, K.J. and Hinz-Schallreuter, I. (1998) Internal structure of Cambrian conodonts. *Journal of Paleontology* **72**, 91–112.
Parkhaev, P. Yu. (1998) Siphonoconcha—a new class of early Cambrian bivalved organisms. *Paleontological Journal* **32**, 1–15.
Peel, J.S. (1991) Functional morphology, evolution and systematics of early Palaeozoic univalved molluscs. *Bulletin Grønlands Geologiske Undersøgelse* **161**, 1–115.
Thomas, R.D.K. and Reif, W.-E. (1993) The skeleton space: a finite set of organic designs. *Evolution* **47**, 341–360.

1.2.3 Cambrian Food Webs

N.J. BUTTERFIELD

Introduction

Food webs are descriptions of who eats whom within a community, thereby tracking energy flow through the system and, to an important degree, characterizing its ecological structure. Clearly any palaeoecological analysis would be greatly served by a detailed accounting of its food web. Nowhere is this more so than in the Early Cambrian when, following approximately three billion years of relatively simple microbially dominated ecologies, large energetic animals were suddenly thrust into the equation. Whatever its ultimate causes, this Cambrian 'explosion' of metazoans necessarily involved a revolution in new types of feeding strategies and a fundamental expansion of ecological interactions. The Proterozoic–Phanerozoic transition thus stands as a unique interval witnessing the construction of modern-style food webs, and their myriad and mutual feedback effects on the environment and biogeochemical cycling. Is it possible to track that development?

All trophic structures are based ultimately on a source of primary productivity which, in the present context, can be considered as that provided by marine photosynthesis. Very simplistically, the energy captured in this process travels up a food chain via herbivores to primary, secondary, and even tertiary carnivores, and is returned to the system via respiration. With an average transfer efficiency of <10% between trophic levels, it is not surprising that food chains leading to large carnivores are characteristically short (typically comprising three or four links; Pimm *et al*. 1991), and that most of the biomass and metabolism of an ecosystem is concentrated near the base of the trophic pyramid. In the real world, of course, most prey have multiple predators and most predators have multiple prey; thus, the overall pattern of metabolic exchange in most communities appears as a reticulate web rather than a simple chain. Moreover, when omnivores, mixotrophs, detritivores, parasites, and other forms that defy simple trophic categorization are included in the equation, as well as a range of *indirect* effects (where the direct effects of one species on another alters the abundance of a third; Menge 1995), the system can become enormously complex. One potential advantage in considering the trophic structure of Early Cambrian communities is that it might represent a stage where the system was still simple. Alpha-level diversity appears to have been relatively low, and many of the complicating effects of scale and specialization are likely to have been limited or absent.

Reconstructing Cambrian trophic structures

Ancient food web analysis faces the fundamental problem of postmortem information loss. Taphonomic processes inevitably produce a fossil assemblage that only dimly mirrors the life assemblage from which it was drawn, and there is the obvious difficulty of determining trophic behaviour solely from fossil morphology. Because most organisms in most environments lack a mineralized skeleton, the exceptional preservation of non-mineralizing organisms necessarily becomes a focus of any detailed palaeoecological analysis (Conway Morris 1986). Within this context, trophic structure can be addressed through a combination of: (1) gut-content analysis; (2) functional morphology, with habit being inferred from mechanical optimality and modern analogues; (3) fossil associations that point to particular trophic relationships; (4) trace fossil analysis, including assessment of coprolite contents and various feeding traces; (5) addition by inference, or a 'fleshing out' of the community based on the recognition of coevolved characteristics (e.g. defensive adaptations imply the presence of predators); (6) inference from phylogeny; and (7) theoretical assessment of food webs.

In level-bottom environments, the most comprehensive palaeoecological analysis has been carried out on the Middle Cambrian Burgess Shale (Conway Morris 1986), but even here there is little direct evidence of trophic linkage. Although the alimentary canals of a number of taxa are preserved, identifiable contents are

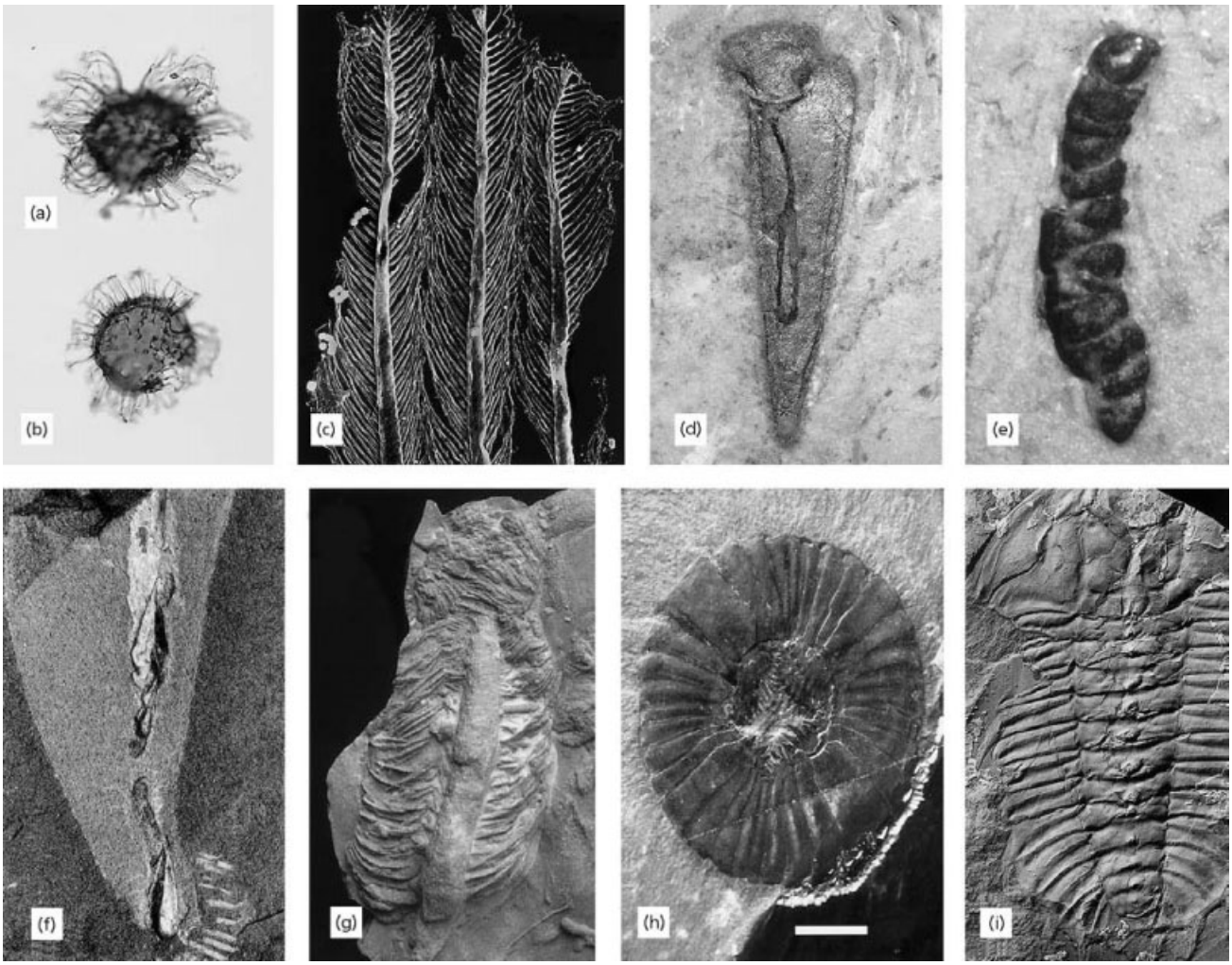


Fig. 1.2.3.1 Representatives of various Early and Middle Cambrian trophic levels. Together these can be arranged as a food chain of up to six tiers, e.g. phytoplankton primary producer (acritarch) → zooplankton herbivore (filter-feeding arthropod) → benthic suspension feeder, possibly a primary carnivore (hyolithid) → benthic secondary carnivore (priapulid) → benthic, possibly tertiary, carnivore (trilobite) → nektonic top predator (anomalocaridid). (a & b) Typical Cambrian acritarchs with a spinose or acanthomorphic ornament, Lower Cambrian, Topiggane Formation, Spitsbergen (courtesy of A.H. Knoll). (c) Arthropod filter apparatus, upper Lower Cambrian, Mount Cap Formation, NW Canada. (d) Hyolithid with simple, sediment-free, phosphatized gut, Middle Cambrian, Mount Cap Formation. (e) Phosphatized faecal string, Middle Cambrian, Mount Cap Formation. (f) Posterior part of priapulid worm *Ottoia* with ingested whole hyolithids, Middle Cambrian, Burgess Shale, SW Canada (courtesy of S. Conway Morris). (g) Hunting trace of arthropod and its prey, an infaunal 'worm', Lower Cambrian, Mickwitzia Sandstone, Sweden (courtesy of S. Jensen). (h) Mouth apparatus of an anomalocaridid, Middle Cambrian, Burgess Shale. (i) Trilobite with non-fatal bite-mark (upper left), Middle Cambrian, Stephen Formation, SW Canada (courtesy of D.M. Rudkin). Scale bar in (h) represents approximately 20 µm for (a) and (b); 10 µm for (c); 2 mm for (d); 1 mm for (e); 5 mm for (f); 10 mm for (g), (h) and (i).

sparse: the gut of the large arthropod *Sidneyia* has been shown to include the remains of a hyolithid, a small trilobite, and comminuted shelly material (possibly bradoriids), whereas the priapulid worm *Ottoia* clearly ingested whole, live hyolithids (Fig. 1.2.3.1f) and may also have engaged in cannibalism. At a slightly lower level of confidence, functional morphology supplemented by phylogenetic inference provides a reasonable measure of trophic status. Thus, acritarchs and algae represent primary productivity in the Burgess Shale community; sponges, chancelloriids, brachiopods, stalked echinoderms, and sea-pen-like forms were engaged in sessile filter-feeding or suspension feeding; the arthropod *Odaraia* was a nektonic suspension-feeder; and various trilobites, chaetognath-like forms, and anomalocaridids were probably carnivores. An association of the lobopo-

dian *Aysheaia* with sponges suggests that it may have been parasitic on them. The remainder (and majority) of the Burgess Shale forms remain poorly resolved trophically, but most likely represent various types of grazers and detritivores.

A detailed quantitative analysis revealed that the Phyllopod Bed community (the erstwhile principal unit of the Burgess Shale) contained most of the trophic habits seen in modern marine communities, though perhaps extending only to the level of primary carnivores (Conway Morris 1986).

Taphonomic bias of course applies to any fossil assemblage, and in the Phyllopod Bed it appears to favour relatively large benthic metazoans: zooplankton and nekton are rare, as are meiofauna and truly soft-bodied forms lacking a recalcitrant cuticle; sedimentary trace fossils are entirely absent. If the dearth of these forms is artefactual, as appears to be the case, then it may be more useful to look at early metazoan ecosystems in a more qualitative way—what trophic interactions can be discerned for the Early to Middle Cambrian as a whole? Discovery of Early Cambrian filter-feeding zooplankton (Fig. 1.2.3.1c), for example, reveals an early and sophisticated metazoan exploitation of the water column; a hyolithid preserved with a simple, sediment-free gut (Fig. 1.2.3.1d) establishes a suspension-feeding habit for these common but enigmatic Cambrian fossils; diverse coprolites (e.g. Fig. 1.2.3.1e)—some containing acritarchs, others comminuted lingulid shells—record the activities of vagrant herbivores and prey-selective carnivores; centimetre-scale vertical burrows packed with skeletal debris are interpreted as the stomach contents of shell-breaking cnidarians (Alpert and Moore 1975); borings, particularly in brachiopod valves, indicate specialized adaptations for penetrating shelled prey (Conway; Morris and Bengtson 1994); intersecting trace fossils suggest that arthropods actively hunted infaunal 'worms' (Fig. 1.2.3.1g; Jensen 1990); and healed injuries on trilobites (Fig. 1.2.3.1i) point to the presence of a large biting predator (often suggested to be an anomalocaridid, although it is difficult to envisage how the *Peytoia* mouthpiece (Fig. 1.2.3.1h) might have effected these particular bites). Taken together, these disparate data point to the likelihood that some Early Cambrian food chains extended to five or six tiers (Fig. 1.2.3.1), and included an overall range of fates and behaviours similar to that in modern food webs. The principal difference between the trophic structures of the Early to Middle Cambrian and Recent would seem to be one of intensity and increasing *breadth* of food webs (as opposed to *length* of food chains). This in turn is likely to be a consequence of increased alpha-level diversity and long-term escalation.

Early evolution of food webs

The simple identification of who eats whom, of course, reveals little about the dynamics of a food web, especially during the evolution of new behavioural repertoires. The direct effects of ecological interactions (e.g. competition, coevolution, escalation, symbiosis, exploitation of vacant ecospace) are well appreciated and have been a principal focus for explaining evolutionary radiations. Studies of modern marine food webs, however, suggest that as much as half of the adjustments a community makes to trophic perturbations derive from *indirect* effects such as keystone predation, trophic cascades, 'apparent competition', and 'habitat facilitation' (Menge 1995), not to mention the broader concepts of key innovations, key species, and 'ecosystem engineering' (Lawton and Jones 1995). Moreover, a recognition that shifts in trophic structure can cascade both down and up food chains multiplies the potential effects of trophic innovation, and raises the issue of whether marine ecology is controlled primarily from the 'bottom up' (i.e. by nutrients, primary productivity, and small organisms) or from the 'top down' (i.e. by predation and larger organisms). If a case can be made for some of these ecological effects—direct or indirect—scaling up to an evolutionary level (Jablonski and Sepkoski 1996), then there is a sound basis for explaining the Cambrian 'explosion' as an ecological phenomenon.

Food webs must have started off simply (i.e. as chains) and been built from the bottom up (e.g. the evolution of carnivores was obviously preceded by that of herbivores, etc.). Thus, for a time, every newly evolved tier served as 'top predator'. The effects of such addition to the top of an accreting trophic pyramid would, in the first instance, have cascaded down, triggering adaptive (presumably defensive) responses in underlying levels. It would also, however, have set the scene for the evolution of yet another tier above. Thus the simple evolution of heterotrophs—a key innovation—may have induced a mutual feedback system of diversification between trophic levels, rapidly escalating to give rise to a fully fledged Cambrian ecosystem (Stanley 1973). Recent advances in Proterozoic palaeontology preclude a blanket application of this 'cropping hypothesis', but it does appear to hold when applied to the Proterozoic–Cambrian plankton record (Butterfield 1997). Notably, the phytoplankton, which represents the vast majority of all marine primary productivity, underwent a major diversification in the Early Cambrian, in marked parallel with the Cambrian radiation of large animals. Since phytoplankton ornamentation (Fig. 1.2.3.1a,b) is invisible to most large animals, it would appear that its sudden diversification was a top-down response to the grazing activities of small animals newly introduced to the plankton. Indeed, alongside the direct evidence of

fossil meso-zooplankton (Fig. 1.2.3.1c), the phytoplankton record itself can be interpreted as a proxy for the evolution of Early Cambrian zooplankton. Zooplankton make up the bulk of animal biomass in modern oceans and, by repackaging unicellular phytoplankton as nutrient-rich particles some 10–100 times as large, link the microscopic world of marine primary productivity to the macroscopic world of large animals. The evolution of meso-zooplankton may thus have been the key innovation behind the Cambrian 'explosion' of large animals.

Although clearly a prerequisite for large animals in the pelagic realm, the effects of zooplankton evolution on benthic ecology are less immediately obvious. Rapid sedimentation of zooplankton faecal pellets has been invoked in the oxygenation of the late Proterozoic sea floor (Logan *et al.* 1995), and would also have enhanced the benthic delivery of labile, nutrient-rich organic compounds (see Section 1.1.4). At the same time, the simple effect of repackaging phytoplankton into much larger particles would have produced a more concentrated and exploitable resource for the contemporaneous benthos. Burrowing, in particular, is likely to have increased in response to the introduction of zooplankton faecal pellets, which in turn would have had profound consequences on the physical, chemical, and biological characteristics of sediments, fundamentally altering the benthic environment. Such far-reaching effects may account for much of the major biogeochemical perturbation that accompanied the Proterozoic–Phanerozoic transition (e.g. C isotope shifts, major phosphogenic events). This is often viewed as a cause of the Cambrian radiations through a bottom-up injection of nutrients, but is more likely—at least in the first instance—to be a top-down consequence of adding the new tier of zooplankton (Butterfield 1997). There are, of course, other behaviours that link the pelagic and benthic realms, although these may be of more limited or local importance. They include benthic suspension feeding, most notably in the widespread development of archaeocyathid reefs in the Early Cambrian, benthic grazing and predation by pelagic organisms (e.g. anomalocaridids), and the activities of planktotrophic metazoan larvae. All of this inevitably resulted in a more closely coupled and mutually dependent plankton and benthos, and an increasingly complex trophic structure. As links multiplied, and food webs increased in breadth and complexity, the strength and predictable consequences of particular links was necessarily reduced. By the same token, however, the stability of the system was surely enhanced as routes through the food web became increasingly varied (cf. McCann *et al.* 1998). Thus, paradoxically, the very simplicity of early metazoan ecosystems made them singularly susceptible to change.

References

Alpert, S.P. and Moore, J.N. (1975) Lower Cambrian trace fossil evidence for predation on trilobites. *Lethaia* **8**, 223–230.

Butterfield, N.J. (1997) Plankton ecology and the Proterozoic–Phanerozoic transition. *Paleobiology* **23**, 247–262.

Conway Morris, S. (1986) The community structure of the Middle Cambrian Phyllopod Bed (Burgess Shale). *Palaeontology* **29**, 423–467.

Conway Morris, S. and Bengtson, S. (1994) Cambrian predators: possible evidence from boreholes. *Journal of Paleontology* **68**, 1–23.

Jablonski, D. and Sepkoski, J.J. Jr (1996) Paleobiology, community ecology, and scales of ecological pattern. *Ecology* **77**, 1367–1378.

Jensen, S. (1990) Predation by early Cambrian trilobites on infaunal worms—evidence from the Swedish Mickwitzia Sandstone. *Lethaia* **23**, 29–42.

Lawton, C.G. and Jones, J.H., eds. (1995) *Linking species and ecosystems*. Chapman and Hall, New York.

Logan, G.A., Hayes, J.M., Hieshima, G.B. and Summons, R.E. (1995) Terminal Proterozoic reorganization of biogeochemical cycles. *Nature* **376**, 53–56.

McCann, K., Hastings, A. and Huxel, G.R. (1998) Weak trophic interactions and the balance of nature. *Nature* **395**, 794–798.

Menge, B.A. (1995) Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecological Monographs* **65**, 21–74.

Pimm, S.L., Lawton, J.H. and Cohen, J.E. (1991) Food web patterns and their consequences. *Nature* **350**, 669–674.

Stanley, S.M. (1973) An ecological theory for the sudden origin of multicellular life in the late Precambrian. *Proceedings of the National Academy of Sciences, USA* **70**, 1486–1489.

1.2.4 The Origin of Vertebrates

M.P. SMITH and I.J. SANSOM

Introduction

Although pre-Silurian vertebrates have been known since the late 1880s, they have generally been considered to be low in diversity and a relatively insignificant prelude to the principal radiation of the group in the Late Silurian and Devonian. Recent discoveries have demonstrated, however, that Ordovician vertebrate faunas are not only more abundant and widespread than hitherto suspected but also contain a far greater diversity of groups. Furthermore, there is now firm evidence that the fossil record of vertebrates extends farther back in time, into the Cambrian, and that their initial radiation was underway during this period.

Ordovician vertebrates were first discovered by the United States Geological Survey in the Harding Sandstone of south-eastern Colorado, USA. The specimens were drawn to the attention of Charles D. Walcott (also

notable for his later discovery of the Burgess Shale), who published a description of the vertebrate fauna in 1892. Reports of Ordovician vertebrate remains from outside North America remained extremely limited, and often erroneous, and it was not until the latter decades of the twentieth century that agnathan remains of this age were firmly identified elsewhere. The first reports were from the Amadeus Basin, Northern Territory, Australia, where complete, articulated specimens of the genus *Arandaspis* are present. A related genus, *Sacabambaspis*, occurs in the Llanvirn of Bolivia and Argentina. These two taxa are united within the Arandaspida (Fig. 1.2.4.1) (Forey and Janvier 1994), the key characters of which include dorsal and ventral headshields formed from single large plates, paired openings to the pineal and parapineal photosensory organs, extreme anterior positioning of the eyes, and multiple branchial ducts covered with protective rhombic plates and arranged in a slanting row. Specimens of *Sacabambaspis* also include details of the oral region, rarely preserved in agnathans, where the lower 'lip' bears a series of finger-like structures, covered in minute scales, that may have opened like a fan to assist in feeding. Disarticulated microvertebrate remains have also been recorded from the Ordovician of Australia, and include arandaspids together with some unassigned forms. Ordovician microvertebrate material is also known from the Timan-Pechora province of Russia and, more equivocally, from North China. However, with the exception of the Harding Sandstone faunas, diversity remains low at all of these localities on the basis of current evidence.

The Harding Sandstone of Colorado

The Harding Sandstone Formation is a thin unit of quartz arenite which was deposited during middle Caradoc (Ordovician) time along the south-eastern flank of the Transcontinental Arch, a ribbon of emergent basement which ran south-west to north-east from Arizona to Wisconsin during the Ordovician. The sediments are exclusively marine, were deposited in an inner shelf to shoreface transition, and contain a fauna which includes cephalopods, bivalves, and conodonts, in addition to the fish fauna. Walcott documented three vertebrate taxa:

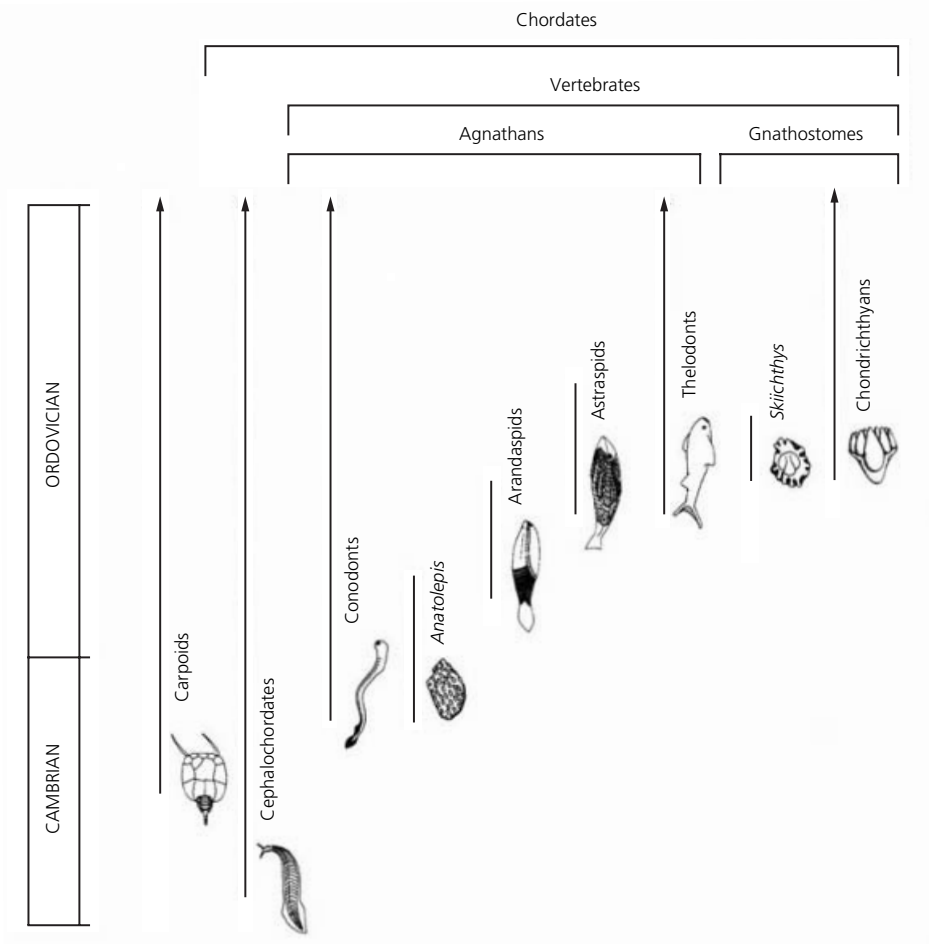


Fig. 1.2.4.1 Stratigraphic distribution of Cambrian and Ordovician vertebrates, together with carpoids and cephalochordates.

Astraspis desiderata, *Eriptychius americanus*, and *Dictyorhabdus priscus*. The last was described by Walcott as the notochordal sheath of a chimeroid chondrichthyan (the group to which extant rat fish and elephant fish are assigned) but subsequent histological investigations have shown that it is not a vertebrate; its zoological affinities remain enigmatic. *Eriptychius* is known from abundant disarticulated exoskeletal fragments, but *Astraspis* is the only genus which is sufficiently well preserved to permit detailed anatomical studies. The taxon differs markedly from the arandaspids of Australia and South America in the possession of a tesserated headshield, open branchial ducts, a covered pineal region, and the presence of dentine and enameloid which forms the raised tubercular ornament of the exoskeletal plates (Sansom *et al.* 1997). *Astraspis* and the arandaspids are not closely related, although both constitute sister groups to a more advanced group of agnathans, the heterostracans (see Fig. 1.2.4.3a) (Forey and Janvier 1994).

Recent micropalaeontological work has revealed that the vertebrate biodiversity of the Harding Sandstone has been considerably underestimated. These studies of individual isolated scales, plates, and fragments have revealed disarticulated remains of at least 10 other taxa, in addition to the heterostracomorph agnathans *Astraspis* and *Eriptychius*, which together comprise some 90% of the residues. Significantly, these not only contribute to an overall increase in species diversity, but also represent the first appearances of a number of major fish groups. One of these taxa, *Skiichthys halsteadi*, has scale morphologies and histology which suggest a relationship with either the acanthodians or placoderms, and indicates the possible presence of gnathostomes (jawed fish) in the Ordovician (Smith and Sansom 1997). Further evidence for the presence of mid-Ordovician gnathostomes comes from shark-like scales which also occur in the sandstone (Sansom *et al.* 1996). Together, these indicate that the origin of gnathostome fish does not form part of the Silurian radiation of fish groups, as traditionally believed, but lies in the early part of the Ordovician.

Cambrian vertebrates

Although the occurrence of a small number of species of Ordovician fish has been accepted since Walcott's original description, the same cannot be said of Cambrian vertebrates, the existence of which has remained hotly disputed. *Anatolepis* was first described from the Valhallfonna Formation (Arenig–Llanvirn, Ordovician) of north-eastern Spitsbergen as a heterostracan agnathan. Fragments of exoskeletal armour assigned to the genus (Fig. 1.2.4.2a) have subsequently been found from a large number of localities in Laurentia, the North American palaeocontinent, in sediments ranging from Late Cambrian to late Early Ordovician age. Although initially described as a vertebrate, *Anatolepis* was not widely accepted as such for many years, with alternative hypotheses of affinity centring on the similarity of the scales to the armour of some merostome arthropods. Histological work on Cambrian and Ordovician material has, however, demonstrated that the ornamented tubercles are formed of typical dentine (M.P. Smith *et al.* 1996), a tissue found only within vertebrates (Fig. 1.2.4.2b). Each tubercle is underlain by a pulp cavity from which dentine tubules radiate before further subdividing to produce a terminal dentine network close to the surface of the scale. The individual tubercles are connected by a lamellar tissue which grew centrifugally and contains

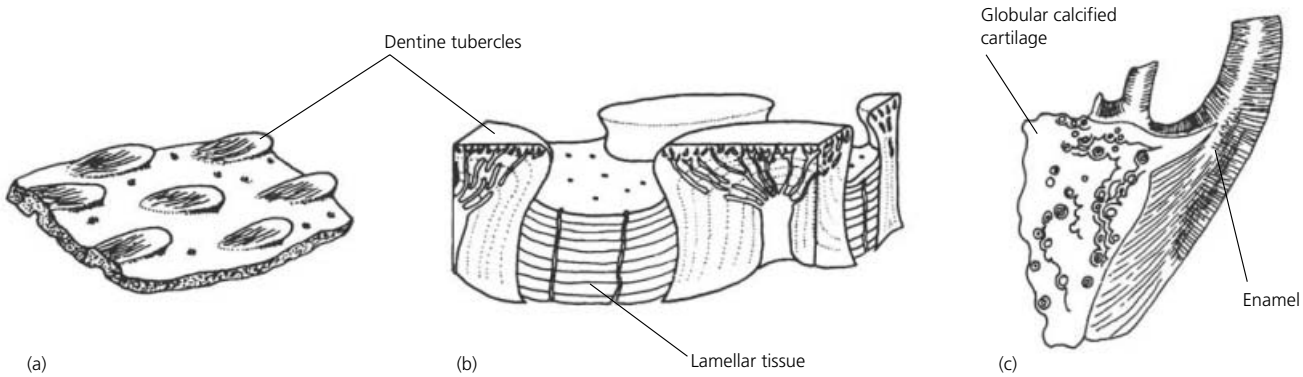


Fig. 1.2.4.2 Cambrian vertebrates. (a) Fragment of exoskeletal armour of the Late Cambrian–Early Ordovician fish *Anatolepis*. (b) Block diagram of the distribution of hard tissues in *Anatolepis*. (c) Line drawing to illustrate tissue distribution in the Late Cambrian–earliest Ordovician conodont *Cordylodus*. (b, After M.P. Smith *et al.* 1996.)

pore canals. Cambrian scales have also been claimed from Australia, but in this case the histology is rather equivocal and confirmation awaits the description of further material. The presence of *Anatolepis*, together with conodonts (see below), in the Late Cambrian demonstrates not only that vertebrates had made their first appearance by the end of the Cambrian, but also that their initial diversification was underway by this time.

Evidence for vertebrates deeper into Cambrian time is scanty and more equivocal, but for more primitive chordate sister groups it is more secure. *Pikaia* from the Burgess Shale is perhaps the most widely known prevertebrate chordate fossil taxon (Fig. 1.2.4.1) and is of probable cephalochordate affinity. Its anatomy is broadly comparable with that of extant cephalochordates (amphioxus) although it does differ in having short protrusions in the pharyngeal area and a pair of anterior tentacles. A recently described, and older, specimen from the Chengjiang Lagerstätte of China (see Section 3.4.3) is closer in size and morphology to extant representatives of cephalochordates, including the presence of multiple narrow pharyngeal openings, through which efferent water passed (Shu *et al.* 1996). *Metaspriggina*, another Burgess Shale taxon, is a third unequivocal Cambrian chordate with preserved soft parts (Simonetta and Insom 1993), but is known only from a single tail and, consequently, is of limited utility in analysing cephalochordate–vertebrate relationships. Most tantalizingly, a single specimen from the Burgess Shale, which has an undoubtedly chordate trunk, also preserves details of the head morphology (Simonetta and Insom 1993). The head resembles, at least superficially, the cartilaginous cranial skeleton of modern lampreys, one of the two groups of living agnathans (Fig. 1.2.4.3). If confirmed, this unnamed specimen demonstrates the presence of unarmoured agnathan vertebrates within the Middle Cambrian and goes some way towards rooting the origin of vertebrates within the Early Cambrian radiation of animal groups.

A confusion of conodonts

For 130 years after their first description in 1856, the affinity of conodonts developed into one of the classical debates in palaeobiology. Conodonts are known almost exclusively from their apatitic tooth-shaped elements and range from the uppermost part of the Cambrian to the end of the Triassic. It is clear that each species possessed a variety of differing morphologies of element, together referred to as an apparatus, and from rare instances of the preservation of intact apparatuses (but without associated soft tissue) it can be inferred that the elements were arranged in a bilaterally symmetrical array which was differentiated from anterior to posterior. With only the morphology of the elements and apparatus as guidance, the group was, inevitably, compared and assigned to a wide variety of organisms, ranging from cnidarians to vertebrates, and even to plants and algae. A majority of the animal groups to which conodonts were assigned possessed biting or grasping structures, and the comparisons were largely ones of functional analogy rather than homology (see Section 4.1.9).

The discovery of the first bona fide soft parts in 1983 rapidly shifted the focus of the debate. A total of 12 specimens of conodonts with preserved soft parts are now known, 10 of which come from the Granton Shrimp Bed of Edinburgh, Scotland (Aldridge *et al.* 1993). Single specimens are also known from the Early Silurian of Wisconsin, USA, and the Late Ordovician of South Africa (see Section 3.4.4), but these add relatively little information regarding the anatomy of conodonts. The Granton conodonts are elongate, 21–55 mm in preserved length, and possessed a laterally compressed trunk with V-shaped myomeres, a notochord, and a ray-supported asymmetrical caudal fin. The apparatus lies along the line of bilateral symmetry with the S and M elements of the ramiform basket at the anterior and two pairs of P elements to the posterior. Two lobate structures at the anterior termination have been interpreted as the supporting cartilages for large eye capsules and other, more equivocally preserved structures have been interpreted as a dorsal nerve cord, otic capsules, and possible branchial structures. On the basis of the soft tissue evidence, conodonts lie crownward of myxinoids (hagfishes) as the sister group of all other vertebrates with biomineralized tissues (Aldridge *et al.* 1993; Donoghue *et al.* 1998).

Histological investigation of conodont elements has revealed a range of hard tissues which are consistent with this phylogenetic relationship. In the majority of conodont taxa, the crowns of elements are composed of apatite crystallites arranged normal to incremental growth lines (Fig. 1.2.4.2c); alternatively, the crystallites may lie obliquely to the growth lines (Sansom *et al.* 1992). The former is identical to vertebrate enamel and the latter is considered to be a homologous tissue (Sansom *et al.* 1992; M.M. Smith *et al.* 1996).

White matter, an additional tissue found within the crown of conodont elements, is currently of enigmatic origin. Cell lacunae and canaliculi have been identified within white matter and it has been postulated that this tissue represents a form of cellular dermal bone (Sansom *et al.* 1992). The lacunae and canaliculi have now been documented from a variety of conodont taxa, and fall within the size range of these structures for vertebrates, but developmental considerations render it unlikely that the tissue is dermal bone.

The cavity within the base of the element is filled, in

different taxa, by a surprising variety of tissues, collectively termed basal bodies. These tissues include both globular calcified cartilage, which directly underlies enamel (Fig. 1.2.4.2c), and dentine; the latter is variably developed across a range of conodont taxa (Sansom *et al.* 1992; M.M. Smith *et al.* 1996). At present, the reason for this histological disparity is not clear. However, the full range of tissues is present in the earliest conodonts (Fig. 1.2.4.2) of Late Cambrian and Early Ordovician age.

The carpoid heterodoxy

An alternative, heterodox, view of early vertebrate evolution and relationships has been propounded by R.P.S. Jefferies in a series of papers over the course of four decades (see Jefferies 1986). On the basis of detailed anatomical studies on carpoids, an extinct group of asymmetrical echinoderm-like animals (Fig. 1.2.4.1), Jefferies has advanced a hypothesis which differs from generally accepted relationships in a number of fundamental ways. Firstly, and most significantly, Jefferies considers tunicates and vertebrates to be more closely related to each other than either is to cephalochordates (Fig. 1.2.4.3c), in contrast to the more conventional view that the cephalochordates are the sister group of vertebrates (Fig. 1.2.4.3b). Secondly, Jefferies claims to be able to identify stem and crown group representatives of all of these terminal taxa within the carpoids. These claims

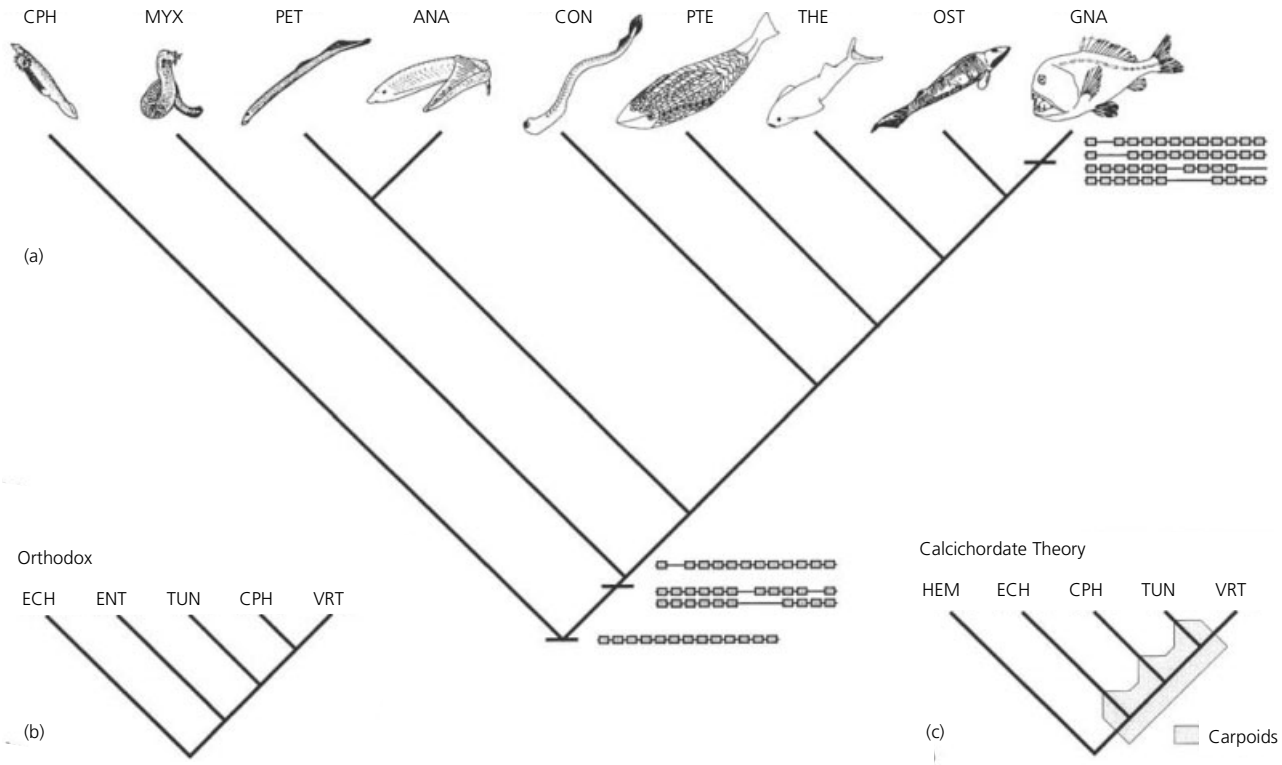


Fig. 1.2.4.3 Proposed phylogenetic relationships of jawless vertebrates and deuterostome sister groups. (a) Phylogenetic relationships of primitive vertebrates with the numbers of homeobox gene clusters indicated. Cephalochordates have a single *Hox* cluster, the primitive condition seen in other phyla. The situation in lampreys is unclear, but they probably have two or three clusters whereas gnathostome vertebrates (jawed fish and crownwards) have four *Hox* clusters. (b) Relationships of higher deuterostome groups obtained in most phylogenetic analyses. The 'hemichordates', comprising enteropneusts and pterobranchs, are generally considered to be polyphyletic and only the enteropneusts are incorporated on this diagram. (c) Relationships of higher deuterostome groups in Jefferies' Calcichordate Theory; the hemichordates are treated as a monophyletic group. Tunicates (represented by extant sea squirts and salps) are considered to be more closely related to vertebrates than either is to cephalochordates. The area of the cladogram occupied by the carpoids in Jefferies' theory is shaded. ANA, anaspids; CON, conodonts; CPH, cephalochordates; ECH, echinoderms; ENT, enteropneust 'hemichordates'; GNA, gnathostomes (jawed vertebrates); HEM, hemichordates; MYX, myxinoids (hagfishes); OST, osteostracans; PET, petromyzontids (lampreys); PTE, pteraspidomorphs (which include *Astraspis*, arandaspids and heterostracans); THE, thelodonts; TUN, tunicates; VRT, vertebrates. (a, After Forey and Janvier 1994 and Meyer 1998.)

have been firmly refuted by echinoderm palaeontologists who tend to view the carpoids as an 'aberrant' group of early echinoderms, but Jefferies' Calcichordate Theory has proved difficult to overturn when details of the morphological data are taken into account. The debate is currently unresolved, but cannot be ignored. A number of lines of argument may be taken in further testing the Jefferies model. Firstly, new discoveries of vertebrates and their relatives in the Cambrian allow a more constrained appraisal of the alternative cladograms and stratigraphic distributions. Chordates, in the form of cephalochordates, first appear in the Lower Cambrian Chengjiang Lagerstätte and vertebrate diversification was certainly underway by the Late Cambrian, as indicated by the presence of both conodonts and *Anatolepis*. In contrast, the most primitive of Jefferies' 'stem vertebrates', *Chinianocarpus*, first appears in the mid-Early Ordovician and *Placocystites*, the most derived, is restricted to the Wenlock. The preservation potential of carpoid calcite skeletons is significantly greater than that of soft-bodied chordates yet, if Jefferies' model is correct, it is the carpoid stratigraphic ranges that are significantly attenuated by non-preservation. Quantitative parsimony tests of the alternative cladograms using stratigraphic data would be a useful contribution to the debate. Secondly, additional, computer-based, cladistic studies of both extant and fossil faunas may go some way toward breaking the current impasse over interpretations of phylogenetic relationships between extant crown groups. At present, a majority produce topologies which have cephalochordates as the sister group of vertebrates, in opposition to the Calcichordate Theory.

Early vertebrate relationships

The application of phylogenetic (cladistic) analysis has greatly facilitated the appraisal of evolutionary relationships amongst early vertebrates (Fig. 1.2.4.3a). Despite this, published cladograms remain relatively unstable in comparison with those derived for higher vertebrate groups and it is probable that this will continue to be the case for some time. Nevertheless, the recent recovery of microvertebrates from Cambrian and Ordovician strata, together with the increasing quantity of soft bodied data available, provide important information regarding the timing and tempo of the initial radiation of vertebrate groups. Similarly, advances in the understanding of homeobox regulatory mechanisms have provided insights into possible underlying developmental controls. *Hox* genes have a fundamental role in the regulation of gene expression relating to the formation of body plans and structural elements, and are probably present in all metazoans. Cephalochordates and most other metazoans possess a single cluster of *Hox* genes, whereas tetrapods possess four, and two investigated groups of teleost fishes have six (Meyer 1998). The situation in agnathan fishes is unclear but it seems that lampreys possess two or three clusters. The duplication events which increase the numbers of *Hox* clusters coincide with major periods of innovation and diversification in the evolutionary record—it is unlikely that they are unrelated but further work is needed to elucidate the interrelationship. In recent years, data from palaeobiology, genetics, and evolutionary developmental biology have contributed to a dramatic change in the understanding of the origin and earliest evolution of vertebrates. It is likely that the continued trend towards integrative work will engender rapid progress towards a fuller understanding of the origin of vertebrates.

References

Aldridge, R.J., Briggs, D.E.G., Smith, M.P., Clarkson, E.N.K. and Clark, N.D.L. (1993) The anatomy of conodonts. *Philosophical Transactions of the Royal Society of London B* **340**, 403–421.

Donoghue, P.C.J., Purnell, M.A. and Aldridge, R.J. (1998) Conodont anatomy, chordate phylogeny and vertebrate classification. *Lethaia* **31**, 211–219.

Forey, P. and Janvier, P. (1994) Evolution of early vertebrates. *American Scientist* **82**, 554–565.

Jefferies, R.P.S. (1986) *The ancestry of vertebrates*. British Museum (Natural History), London.

Meyer, A. (1998) Hox gene variation and evolution. *Nature* **391**, 225–227.

Sansom, I.J., Smith, M.P., Armstrong, H.A. and Smith, M.M. (1992) Presence of the earliest vertebrate hard tissues in conodonts. *Science* **256**, 1308–1311.

Sansom, I.J., Smith, M.M. and Smith, M.P. (1996) Scales of thelodont and shark-like fishes from the Ordovician of Colorado. *Nature* **379**, 628–630.

Sansom, I.J., Smith, M.P., Smith, M.M. and Turner, P. (1997) *Astraspis*—the anatomy and histology of an Ordovician fish. *Palaeontology* **40**, 625–643.

Shu, D.G., Conway Morris, S. and Zhang, X.L. (1996) A *Pikaia*-like chordate from the Lower Cambrian of China. *Nature* **384**, 157–158.

Simonetta, A.M. and Insom, E. (1993) New animals from the Burgess Shale (Middle Cambrian) and their possible significance for the understanding of the Bilateria. *Bolletino Di Zoologia* **60**, 97–107.

Smith, M.M. and Sansom, I.J. (1997) Exoskeletal microremains of an Ordovician fish from the Harding Sandstone of Colorado. *Palaeontology* **40**, 645–658.

Smith, M.M., Sansom, I.J. and Smith, M.P. (1996) 'Teeth' before armour: the earliest vertebrate mineralized tissues. *Modern Geology* **20**, 303–319.

Smith, M.P., Sansom, I.J. and Repetski, J.E. (1996) Histology of the first fish. *Nature* **380**, 702–704.

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1.3 Palaeozoic Events

1.3.1 Ordovician Radiation

A.I. MILLER

Introduction

It has long been known that the first major burst of global diversification among marine animals took place early in the Palaeozoic Era, but the complexity of this interval has become apparent only more recently. The diversification is divisible roughly into two major components: the Cambrian explosion and the Ordovician radiation. Whereas the Cambrian explosion and its Vendian antecedent were characterized by the origin and initial diversification of basic body plans at the phylum and class levels, the Ordovician radiation was manifested mainly by an unprecedented burst of diversification at lower taxonomic levels. During the Ordovician Period, there was a three- to four-fold increase in the global richness of marine animal families and genera relative to Cambrian levels. Moreover, there was a fundamental transition in the overall composition of the marine biota: as the period progressed, the relative contributions of trilobites and other organisms characteristic of the Cambrian fauna declined in the face of a substantial diversification of articulate brachiopods, stenolaemate bryozoans, stalked crinoids, and other groups that dominated Palaeozoic assemblages thereafter. Gastropods, bivalves, and other taxa that would come to dominate sea floors in the post-Palaeozoic also experienced appreciable Ordovician diversification.

Despite the pattern of continuous diversity increase and transition in taxonomic composition that is apparent at the global scale through most of the Ordovician, there is growing evidence that this does not simply reflect the activity of global-scale processes operating at the rates implied by synoptic diversity compilations. Instead, the global signal may represent the sum of disparate transitions taking place around the world in response to local or regional causes (Miller 1997). To investigate this and other issues, researchers worldwide have sought to deconstruct the global Ordovician signal into its geographical, environmental, and morphological components. Data for these studies have been compiled both from the worldwide literature and from a new generation of field, laboratory, and systematic work tailored to address questions of biodiversity at local or regional scales in the light of the global signal. In addition, the Ordovician has been a focal point for studies that have sought to evaluate diversification through quantitative assessment of morphological diversity (disparity: see Section 5.1.3), rather than through the more traditional metric of taxonomic richness. Because of this activity, the Ordovician radiation is becoming something of a proving ground for understanding how a major, long-term diversity transition transpires.

Dissection of the global pattern

When Ordovician diversity patterns among higher taxa at the global scale are more finely subdivided temporally or taxonomically, they exhibit attributes not appreciated fully in coarser treatments. Trilobite families and genera, for example, exhibited a pronounced global transition through the Ordovician (Adrain *et al.* 1998): families and genera belonging to a group that collectively dominated trilobite biotas during the earliest Ordovician (dubbed the 'Ibex' fauna after the earliest of the four North American epochs) declined steadily in taxonomic diversity through most of the Ordovician, giving way to another group of families and constituent genera that diversified appreciably in the Middle and Late Ordovician (dubbed the 'Whiterock' fauna, after the second of the four North American Ordovician epochs). The Whiterock fauna alone contributed to trilobite diversity after the Late Ordovician mass extinction. The reasons for these different evolutionary patterns are not yet understood entirely, but the two faunas apparently flourished in different geographical and environmental regimes, and exhibited different rates of evolution. On these bases, the traditional global paradigm of evolutionary faunas, which places trilobites in the Cambrian evolutionary fauna and tends to view the class as broadly in decline after the Cambrian, should be amended to accommodate the recognition that the Whiterock fauna was diversifying, rather than declining, during the Ordovician.

Geographical and palaeoenvironmental variations

The foregoing discussion not only illustrates the need to continue evaluating the details of diversification at the global level, but also points to the importance of understanding the extent to which these patterns varied geographically or environmentally. The radiation of the Whiterock trilobite fauna, for example, was more appreciable at low latitude than at high latitude (Adrain *et al.*

1998). In a similar vein, substantial latitudinal and environmental differences in Ordovician diversification have now been recognized among a broad range of biotas. For example, there were significant Lower to Middle Ordovician faunal differences among two western Argentinean basins that are currently in close proximity, but which were isolated from one another during the Early and Middle Ordovician (Waisfeld and Sánchez 1996). In the carbonate-dominated Precordillera Basin, which likely comprised a microcontinent located at low latitude, articulate brachiopods and sponges were the predominant faunal elements. By contrast, the siliciclastic-rich Northwestern Basin, which was part of the Gondwanan supercontinent at high latitude, contained a fauna rich in trilobites and molluscs. Clearly, these faunal differences were consequences of differences in climate and depositional regimes among the two regions. With respect to the dynamics of the Ordovician radiation, they illustrate the extent to which the timing and nature of major biotic transitions varied from region to region.

More broadly, diversification throughout the Ordovician differed significantly among Ordovician palaeocontinents (Miller 1997). This may have been attributable, in part, to differences among palaeocontinents in their geological attributes, including the extent of siliciclastic influx. For example, by the late Middle and Late Ordovician, Laurentia (much of present-day North America) contained an abundant and diverse bivalve fauna, whereas South China did not (Fig. 1.3.1.1). Bivalves first diversified in siliciclastic settings at high latitudes, but did not begin to flourish in Laurentia until later, as part of the 'globalization' of the class (Babin 1993). The lack of a similar diversification in South China may have reflected its geology. The level of siliciclastic influx in eastern Laurentia increased significantly during the Middle and Late Ordovician because of the onset of the Taconic orogeny, whereas South China did not experience nearly as extensive an increase in siliciclastics in the absence of similar orogenic activity.

Abrupt local and regional transitions

It is not surprising that various Ordovician biotas exhibited a propensity to occur in particular palaeoenvironments or climatic regimes. However, investigations of the Ordovician radiation have served to illustrate the extent to which the presence, as well as the waxing or waning, of different physical milieus can affect biodiversity. That the patterns observed in global diversity compilations may owe their generation to such transitions is perhaps best illustrated by considering biotic transitions at the local or regional levels. For example, an abrupt

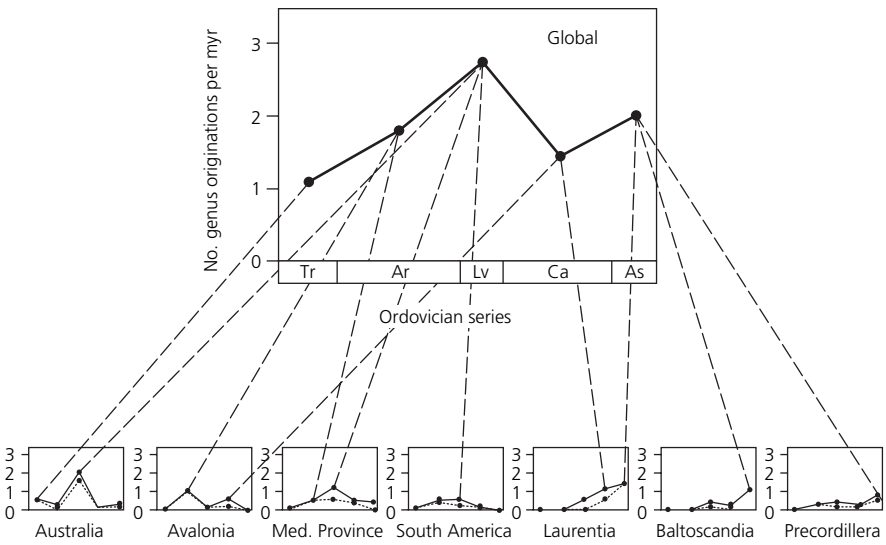

Fig. 1.3.1.1 Patterns of bivalve genus origination among palaeocontinents during the Ordovician radiation, in comparison with the global pattern. Dashed lines illustrate instances in which bivalve diversity for a particular palaeocontinent contributed appreciably to the global time series. Two time series can be distinguished in the palaeocontinental graphs. In each case, the upper curve depicts rates of bivalve first appearance regardless of whether the genera first appeared earlier on another palaeocontinent (i.e. immigration plus origination); the lower curve depicts rates of first appearance only for genera that originated on the palaeocontinent. Data for determining origination rates per million years are from a database of Ordovician genus occurrences, updated from a version described by Miller (1997) and other papers. Abbreviated series designations are for the five series of the updated British standard: Tr, Tremadocian; Ar, Arenigian; Lv, Llanvirnian; Ca, Caradocian; As, Ashgillian.

Middle Ordovician transition among biotas of eastern North America was associated with the onset of the Taconic orogeny: a biota that flourished in warm tropical settings was replaced by one adapted to the cooler, more turbid conditions brought about by the local effects of the orogeny (Patzkowsky and Holland 1993). In this instance, elements of the older biota survived elsewhere in warmer waters, and repopulated part of the study area when suitable conditions returned.

A similarly abrupt biotic transition is recognized at the base of the Middle Ordovician in the Great Basin of western North America (Droser *et al.* 1996). There, articulate brachiopods and other faunal elements increased greatly in abundance, relative to trilobites. Moreover, the contributors to trilobite diversity changed significantly in the interval, at least partly in concert with broader, global transitions (Adrain *et al.* 1998). Combined with the case described earlier for the Middle Ordovician of eastern North America, the pattern in the Great Basin points to the need to further investigate regional patterns around the world, in order to determine the extent to which such transitions permeate Ordovician strata. It may be that the gradual biotic transitions apparent in global compilations of taxonomic diversity were actually built of abrupt, physically induced transitions, the timing of which varied from region to region around the world, thereby imparting the gradual global appearance (see Miller 1998). For understanding the causes of the Ordovician radiation, this distinction is crucial. If the global pattern is also recognizable from region to region around the world, it would suggest that the causes of the radiation were global in scope. Alternatively, if the global signal is the aggregate record of varying regional patterns with unique explanations, a different view emerges. The ongoing investigations of Ordovician strata worldwide should reveal the extent to which the radiation was controlled by local or regional vs. global processes. In this context, the radiation should provide an excellent object lesson concerning the relationships among diversification patterns at different scales.

Morphological diversity

Although the majority of research on the Ordovician radiation has focused on the assessment of taxonomic diversity, a significant new avenue of enquiry is emerging: the analysis of morphological diversity (disparity: see Section 5.1.3), based on direct morphological measurement and statistical analysis of large numbers of the constituents comprising a higher taxon. When compared to and contrasted with taxonomic diversity, temporal patterns of morphological diversity for a higher taxon may provide a different perception of its evolutionary dynamics. For example, analyses of trilobite cranidia have revealed that the morphological diversity of trilobites increased from the Early Ordovician into the Middle and Late Ordovician, whereas the overall taxonomic richness of trilobites declined through the same interval (Foote 1993). Thereafter, trilobite taxonomic diversity continued to fall, but morphological diversity did not decline substantially until after the Devonian. The Ordovician patterns contrast strongly with those exhibited during the Cambrian: the Cambrian increase in taxonomic diversity actually took place in conjunction with declining morphological diversity from the Early Cambrian into the Middle and Late Cambrian (Foote 1993). This further enhances the view that the Ordovician radiation was rather different from the Cambrian explosion.

By categorizing morphological attributes based on whether they were external or internal features of the skeleton, it becomes possible to gain additional insight into the constraints on diversity (Wagner 1995). During the early radiation of gastropods, including the Early Ordovician, diversification was accompanied by a more substantial degree of morphological change than it was thereafter. Beyond that, it has been suggested that external features more likely reflect ecological attributes of the organism than internal features, which would be expected to more directly reflect phylogeny. Over seven time intervals from the Late Cambrian to the Silurian, there was a continuous decline in the magnitude of morphological change among internal features, but, following a precipitous Early Ordovician drop, there was no such decline among external features. On this basis, it appears that the constraints on morphology were primarily phylogenetic rather than ecological (Wagner 1995).

Implications for other Phanerozoic intervals

The research highlighted herein springs directly from a wealth of questions posed by the earlier, more synthetic studies of the 1970s and 1980s. Against the backdrop of these efforts to synthesize and quantify at the global scale, it might seem odd that the focus in the 1990s shifted back to local and regional levels. And yet, there is a fundamental difference between local research in the 1990s and that from an earlier research era. Local research today is almost always conducted with a desire to understand how some regional biota relates to issues of global significance. It is research conducted with a broader objective, instead of being an end in itself.

In this respect, the cumulative record of research on the Ordovician radiation provides an excellent model for efforts focused on other Phanerozoic intervals. Although other intervals were characterized by different species than those that dominated the Ordovician, large-scale biotic transitions have occurred repeatedly throughout the Phanerozoic and may have been governed, broadly,

by the same mechanisms that caused the Ordovician transitions. For example, on a global scale, the Devonian Period was characterized by the initial decline of the Palaeozoic evolutionary fauna, which was dominated by immobile, suspension-feeding faunal elements. It has been suggested that the decline of taxa with this lifestyle was caused by interactions with diversifying, deep-burrowing deposit-feeding organisms; among other things, the deposit-feeders are thought to have undermined the substrates upon which the suspension-feeders lived. However, as an alternative, the transition might not have been caused by these sorts of direct interactions, but rather by local and regional changes to physical habitats that were detrimental to suspension-feeders and favourable to deposit-feeders. From an environmental perspective, orogenic activity increased in several regions during the Devonian to an extent that, in some instances, dwarfed Ordovician tectonic events. The erosion of uplifted source areas produced substantial influxes of siliciclastic sediments that would have favoured the infiltration and diversification of deposit-feeders. If this was the case, the transition should be manifested regionally in Devonian strata as relatively abrupt stratigraphic transitions from carbonate to siliciclastic sedimentation, with concomitant changes in faunal composition to a deposit-feeding biota.

Thus, a common theme for the Ordovician, Devonian, and the rest of the Phanerozoic is that a better understanding of the causes of global biotic transitions may require their dissection into local and regional components.

References

Adrain, J.M., Fortey, R.A. and Westrop, S.R. (1998) Post-Cambrian trilobite diversity and evolutionary faunas. *Science* **280**, 1922–1925.

Babin, C. (1993) Rôle des plates-formes gondwaniennes dans les diversifications des mollusques bivalves durant l'Ordovicien. *Bulletin de la Société Géologique de France* **164**, 141–153.

Droser, M.L., Fortey, R.A. and Li, X. (1996) The Ordovician radiation. *American Scientist* **84**, 122–132.

Foote, M. (1993) Discordance and concordance between morphological and taxonomic diversity. *Paleobiology* **19**, 185–204.

Miller, A.I. (1997) Dissecting global diversity patterns: examples from the Ordovician radiation. *Annual Review of Ecology and Systematics* **28**, 85–104.

Miller, A.I. (1998) Biotic transitions in global marine diversity. *Science* **281**, 1157–1160.

Patzkowsky, M.E. and Holland, S.M. (1993) Biotic response to a Middle Ordovician paleoceanographic event in eastern North America. *Geology* **21**, 619–622.

Wagner, P.J. (1995) Testing evolutionary constraint hypotheses with early Paleozoic gastropods. *Paleobiology* **21**, 248–272.

Waisfeld, B.G. and Sánchez, T.M. (1996) 'Fauna Cámbrica' versus 'Fauna Paleozoica' en el Ordovícico Temprano del oeste de Argentina: interacción entre provincialismo y ambiente. *Geobios* **29**, 401–416.

1.3.2 Rise of Fishes

J.A. LONG

Introduction

Fishes are generally defined as free-swimming aquatic vertebrates which have fins and respire through gills. The earliest fossil fishes, however, are not easily recognized by their body and fin shapes, but by the possession of bone, an organically mineralized tissue which supports and protects the soft tissues and allows for more efficient attachment of muscles (Fig. 1.3.2.1). The advent of bone heralded the onset of great diversity of the first jawless fishes, the agnathans (Long 1995).

The oldest fishes

The oldest definite fossil vertebrates are the remains of scales composed of bone-like tissues from the Late Cambrian Georgina Basin of central Queensland, Australia (Young *et al*. 1996). Early Ordovician fish remains from central Australia include several forms known from scales, such as *Areyongia* and *Apedolepis* (Young 1997). The first well-preserved impressions of complete jawless fish armours occur in the Middle Ordovician of Australia. *Arandaspis* had well-developed dorsal and ventral bony shields, with distinct rows of squarish branchial plates over the gills. It was a precursor to the more successful heterostracan fishes, like *Pteraspis*, which had a single branchial plate covering the gills. Such fishes were prevalent in Silurian and Early Devonian seas, and to a lesser extent, freshwater habitats, largely occupying the niches of benthic detrital and filter feeders. The bone of heterostracans lacked bone cells, and has been termed 'aspidin'. (See Section 1.2.4 for more details on the origins of vertebrates.)

Agnathan diversity

Many kinds of jawless fishes evolved throughout the Silurian and Devonian (Fig. 1.3.2.2). These include armoured forms with a scoop-shaped solid bony shield like the osteostracans (e.g. *Cephalaspis*), the naked lamprey-like anaspids (e.g. *Jaymoytius*), and the heavily scaled thelodonts (e.g. *Thelodus*). Finds from Canada indicate that some thelodonts, the Furcacaudiformes, had laterally compressed bodies with well-developed stomachs (Wilson and Caldwell 1998). Thelodonts in general had an internal soft anatomy (evidenced by impressions in *Thelodus*) suggesting close affinity to jawed fishes (gnathostomes). All early agnathans had

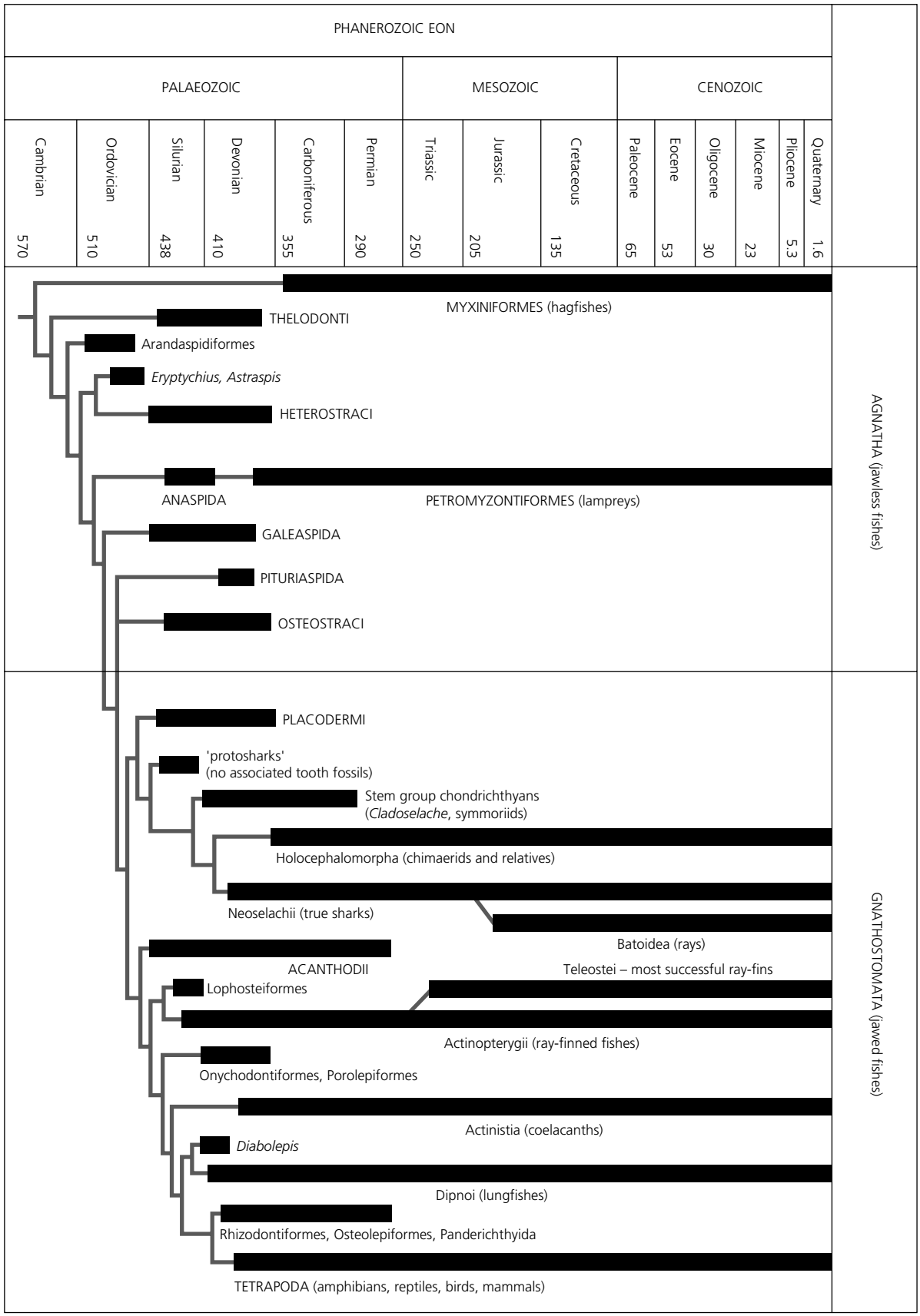

Fig. 1.3.2.1 Major radiations of fish groups through time.

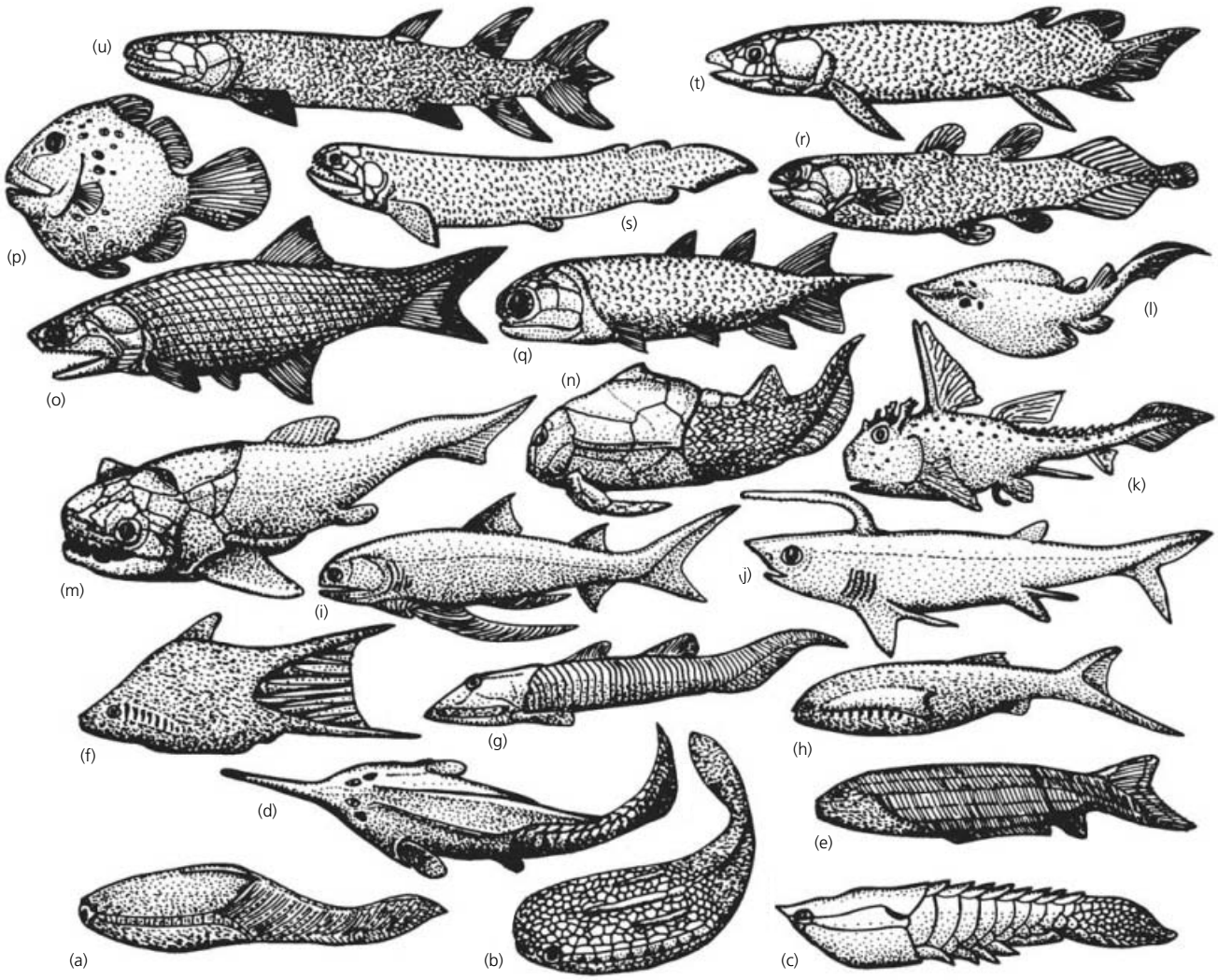

Fig. 1.3.2.2 Diversity of major fish groups through time (a–h, agnathans; i–u, gnathostomes). (a) *Arandaspis* (Arandaspidiformes; Ordovician). (b) *Eriptychius* (Astraspidiformes; Ordovician). (c) *Anglaspis* (Heterostraci; Silurian). (d) *Pituriaspis* (representing Pituriaspida and Galeaspida; Devonian). (e) *Birkenia* (Anaspida; Silurian). (f) *Furcacauda* (Furcacaudiformes; Devonian). (g) *Ateleaspis* (Osteostraci; Silurian). (h) *Thelodus* (Thelodontida; Silurian). (i) *Gyracanthides* (Acanthodii, Climatiiformes; Devonian–Carboniferous). (j) *Falcatus* (Chondrichthyes, Selachii; Carboniferous). (k) *Echinochimaera* (Chondrichthyes, Holocephalomorphi; Carboniferous). (l) *Rhinobatis* (Chondrichthyes, Selachii, Batoidea; Jurassic–Recent). (m) *Mcnamaraspis* (Placodermi, Arthrodira; Devonian). (n) *Sherbonaspis* (Placodermi, Antiarchi; Devonian). (o) *Mimia* (Osteichthyes, basal Actinopterygii; Devonian). (p) *Eoplectus* (Osteichthyes, Actinopterygii, Teleostei; Eocene). (q) *Strunius* (Osteichthyes, Onychodontiformes; Devonian). (r) *Hadronector* (Osteichthyes, Coelacanthiformes; Carboniferous). (s) *Strepsodus* (Osteichthyes, Rhizodontiformes; Carboniferous). (t) *Dipterus* (Osteichthyes, Dipnoi; Devonian). (u) *Eusthenopteron* (Osteichthyes, Osteolepiformes; Devonian).

well-developed sensory-line systems. Osteostracans possessed fields of sensory organs along the sides and top of their shields.

The osteostracan fishes appear to be the closest group to the gnathostomes because they share perichondral bone enveloping the braincase, a large median head vein, and true bone with cell sites (Forey and Janvier 1993). The headshields of osteostracan fishes indicate that the first gill arches were well forward of the eyes, immediately above the mouth. Osteostracans presumably had cartilaginous gill arch supports, as shown by impressions of gill structures on the visceral surface of their shield. Primitive agnathans, like heterostracans, lacked pectoral and pelvic fins. These are found in anaspids as extensions of the fin-folds, but only osteostracans had muscular pectoral fins which were internally attached to a cartilaginous ossification, the scapulocoracoid.

The origins of jaws

Jaws may have first originated in fishes by modification of the front gill arch support bones. The first primitive set of jaws and teeth would have formed when dermal scales, with a tooth-like structure and shape, invaded the mouth and pharynx. Primitive jawless fishes had many more paired gill arches than the jawed fishes; some anaspids possessed 20 or more paired gill pouches. Some agnathans had tooth-like scales lining the buccal cavity (e.g. thelodonts) which could have acted as 'prototeeth' in the reduction of food. Furthermore, the dermal scales of most jawless fishes are constructed of dentinous tissues underlying the enameloid crown, with a bony base. Thelodonts even have a pulp cavity in the base of the scales, making these scales practically 'teeth' in terms of their histology.

The appearance of jaws should naturally herald the abundant appearance of teeth in the fossil record at the same time. Gnathostomes (jawed vertebrates) include the first fishes with jaws and teeth: chondrichthyans, acanthodians, placoderms and osteichthyans, and their evolutionary descendants, the tetrapods (amphibians, reptiles, birds, mammals). Sharks, for example, have hundreds of teeth in their mouths which they grow and shed continuously through life. The average modern shark may shed up to 20000 teeth into the sediment, although Palaeozoic sharks may not necessarily have shed as many teeth as modern forms. Shark skin contains thousands of tiny placoid scales which are also shed into the sediment after death, and readily identified as fossils.

Early sharks and their relatives

The oldest shark-like scales come from the Late Ordovician Harding Sandstone of North America (see Section 1.2.4) and the Early Silurian of Mongolia, yet the oldest shark teeth are of lowest Devonian age, some 30 million years later. As the numbers of teeth and scales are both high per individual shark, the absence of shark teeth in Silurian strata would seem to be a real observation, suggesting that the first sharks had scales of recognizable morphology, akin to those of modern sharks, yet they probably lacked teeth. The appearance of the first teeth most likely correlates with the evolution of jaws in sharks.

Sharks possibly first arose by the Early Devonian in Gondwana, where their teeth are commonly found in some deposits (e.g. Spain, Australia, Antarctica, South America). The Middle Devonian Aztec Siltstone of Antarctica has an unusually high diversity of sharks in both species' numbers and size of teeth, suggesting that Gondwana may well have been the place where toothed sharks underwent their first major radiation. By the Middle Devonian sharks teeth are commonly found throughout the world, and by the Late Devonian more than 50 species are known. The first of the modern sharks, or neoselachians, may date back as far as the Middle Devonian, represented by teeth of *Mcmurdodus* which have multilayered enameloid. *Hamiltonichthys*, from the Lower Carboniferous, was the oldest of the hybodontid shark lineage, a group prevalent in the Mesozoic Era. In the Lower Carboniferous some very large sharks had evolved, like *Edestus giganteus*, from North America, which possessed serrated teeth up to 7–8 cm high on a continuous whorl. Such megapredators would have reached 6 m or more in length. Another major chondrichthyan group, the holocephalomorphs, represented today by the chimaerids and rabbitfishes, appeared in the early Carboniferous. Some sharks of this time, like the petalodonts, had unusual crushing or nipping teeth, possessing few sets in the jaws.

Sharks radiated and diversified throughout the late Palaeozoic and Mesozoic. The largest Palaeozoic predatory sharks may have been the edestids, like *Helicoprion*, whose coiled tooth whorls occur in the middle Permian. If these large whorls sat on the tip of the lower jaws, estimated sizes of 10 m would not be unlikely for these sharks. Huge lamnid sharks evolved in the mid Tertiary, like *Carcharocles megalodon* with teeth 18 cm high, suggesting a total body length of about 15 m.

Acanthodians

The oldest fishes with jaws and teeth preserved intact are the acanthodians, which date back to the Early Silurian. They are often represented in microscopic residues from dissolved limestone as isolated teeth, scales, and fin spines. Acanthodians have been likened to 'spiny sharks' in past literature, although their

affinities appear to lie closer to the higher jawed fishes, such as osteichthyans (true bony fishes), because of scale structure and the gross morphology of their braincase. The oldest acanthodians include forms with distinct gnathal bones on to which strong teeth are ankylosed. This group, the ischnacanthids, were moderately large predators in the Early Devonian seas; some, like *Xylacanthus grandis* from Spitsbergen, reached sizes of 2–3 m. The climatiforms (e.g. *Climatius*) had elaborate dermal shoulder girdle armour and some had many additional spines along the ventrolateral ridge of the body. Acanthodiforms, such as *Acanthodes*, were filter-feeding forms which lacked shoulder girdle armour and had extensive gill rakers for sifting food; they also possessed otoliths (ear stones) for improving 'balance' during swimming manoeuvres. The group survived until the end of the Permian Period.

Placoderms

The most successful of all the early jawed fishes were undoubtedly the placoderms, which appeared in the Early Silurian and reached a peak of diversity during the Middle–Late Devonian. Their name means 'plated skin', referring to a mosaic of bony armour plates that enveloped their heads and trunks. They possessed shark-like tails and in their overall anatomy were much akin to chondrichthyans. Placoderms have alternatively been placed as possible relatives of the bony fishes (osteichthyans) because of their dermal bones and internally ossified braincases. However, the teeth which developed on placoderm jaw bones were not real teeth with roots set into a discrete jaw bone, like those of the osteichthyan fishes, but well-developed pointed cusps that protruded from the jaw bone itself. Placoderms exhibit a multitude of dentition types, revolving around rows of pointed cusps on gnathal bones, or clusters of small denticles or pointed cusps on sheets of bone.

The largest group of placoderms were the arthrodires, which includes the biggest forms, the dinichthyids (e.g. *Gorgonosteus*) reaching 6 m or more. The small antiarchs had external bone-covered props for pectoral fins. One of these, *Bothriolepis*, was ubiquitous in the Middle–Late Devonian, and is represented by over 100 species worldwide. Other groups include the flattened ray-like rhenanids and their heavily armoured relatives the acanthothoracids, the petalichthyids, and the flattened phyllolepids. Placoderms can often be identified from isolated remains because of their unusual plate shapes and dermal ornamentation, making them useful in Devonian biostratigraphic and biogeographical studies. The placoderms became extinct at the end of the Devonian Period, possibly being displaced by the increasing diversity of chondrichthyans.

Osteichthyans

The osteichthyans (true bony fishes) appeared by the Late Silurian, represented by isolated scales, teeth, and rare isolated bones of small ray-finned and lobe-finned fishes. The Osteichthyes comprise: the ray-fins (Actinopterygii), which today form more than 99% of all living fishes and are represented by over 23 000 species (e.g. trout, salmon); and the Sarcopterygii, which have muscular, fleshy lobed fins and include the lungfishes (Dipnoi), and the 'crossopterygians' (a paraphyletic mixture of groups). Although there is only one surviving species, the coelacanth *Latimeria chalumnae*, the 'crossopterygians' include many extinct groups that diversified during the middle Palaeozoic (e.g. Onychodontiformes, Porolepiformes, Osteolepiformes).

The ray-finned fishes were represented in the Devonian by primitive palaeoniscoids like *Cheirolepis* and *Mimia*. The group radiated rapidly by the beginning of the Carboniferous, and over 50 families are known during the late Palaeozoic. Most of the heavily scaled primitive forms gave way to those having thinner round scales, with less rigid cheek and jaw bone arrangements; this enabled more efficient feeding and respiratory mechanisms, such as the buccal-pump system, to evolve. This line of evolution saw the rise of holostean and subholostean fishes in the late Palaeozoic (today represented by gars and bowfins, e.g. *Amia*, *Lepisosteus*) and the first of the modern ray-fins, the teleosteans, by the Late Triassic. Teleosteans have advanced tail fin skeletons with many supporting bones, plus mobile cheeks and detached jaw bones. Their first gill arch (hyoid), which supports the jaws, is often vertically or forwardly inclined. Many of the modern families of fishes had appeared by the close of the Cretaceous Period, and the first teleosteans adapted specifically to life on reefs had appeared by the Eocene Period.

In the Devonian Period the most diverse group of bony fishes were the sarcopterygians (over 100 species); the ray-fins were only a minor component of fish faunas (about 10 species). The earliest sarcopterygians had a shiny tissue, cosmine, that covered the dermal bones and scales and was lost in more advanced lineages. Cosmine may have functioned as an electrosensory tissue.

The ability to gulp air and transgress environmental boundaries evolved only within lungfishes during the Middle Devonian (e.g. *Dipterus*), becoming prominent in the Late Devonian. This gave them an edge on other groups, with later forms developing a further enhanced survival strategy—the ability to aestivate (e.g. *Gnathorhiza*). Lungfishes diversified into forms with crushing tooth plates (e.g. *Chirodipterus*) and others with denticulated palates (e.g. *Griphognathus*, Campbell and Barwick 1987). Post-Devonian lungfishes were largely freshwater forms. Today there are three living lungfish

genera, the most primitive of which is *Neoceratodus forsteri* from Australia which dates back to the Cretaceous Period.

Some of the advanced osteolepiform fishes appear to have developed the ability to breathe air independently, as they had evolved a palatal nostril (a choana) by the Middle Devonian (Long *et al.* 1997). Osteolepidids were a common component of most Devonian fish faunas, in many cases taking the role of top predator. More advanced osteolepiforms, like *Eusthenopteron*, from the Late Devonian of Canada, lost the cosmine layer and had rounded scales (Jarvik 1980). The largest of these predatory lobe-fins were the rhizodontiforms, which dominated the lakes and rivers of the Carboniferous Period. Forms like *Rhizodus* may have reached 6–7 m in length.

The panderichthyid fishes are morphologically closest to the elpistostegalid amphibians, known from Scotland and Russia, in having identical skull-roof patterns, pectoral and pelvic girdles, and endoskeletons which approach the morphology of the basic tetrapod limbs more closely than any other fish. A primitive rhizodontid pectoral skeleton (*Sauripterus*) with eight fin radials supporting the pectoral fin has been described from North America. This matches the eight digits occurring in the limbs of the Devonian amphibian *Acanthostega*. The first tetrapods evolved by the end of the Frasnian stage of the Late Devonian, and at least eight genera had appeared by the close of the Devonian Period.

References

Campbell, K.S.W. and Barwick, R.E. (1987) Palaeozoic lungfishes—a review. *Journal of Morphology* **1** (Suppl.), 93–132.

Forey, P.L. and Janvier, P. (1993) Agnathans and the origin of jawed vertebrates. *Nature* **361**, 129–134.

Jarvik, E. (1980) *Basic structure and evolution of vertebrates*. Academic Press, New York.

Long, J.A. (1995) *The rise of fishes—500 million years of evolution*. University of New South Wales Press, Sydney and Johns Hopkins University Press, Baltimore.

Long, J.A., Campbell, K.S.W. and Barwick, R.E. (1997) Osteology and functional morphology of the osteolepiform fish *Gogonasus andrewsae* Long, 1985, from the Upper Devonian Gogo Formation, Western Australia. *Records of the Western Australian Museum* **53** (Suppl.), 1–89.

Wilson, M.V.H. and Caldwell, M.W. (1998) The Furcacaudiformes: a new order of jawless vertebrates with thelodont scales, based on articulated Silurian and Devonian fossils from northern Canada. *Journal of Vertebrate Paleontology* **18**, 10–29.

Young, G.C. (1997) Ordovician microvertebrate remains from the Amadeus Basin, central Australia. *Journal of Vertebrate Paleontology* **17**, 1–25.

Young, G.C., Karatajute-Talimaa, V.N. and Smith, M.M. (1996) A possible Late Cambrian vertebrate from Australia. *Nature* **383**, 810–812.

1.3.3 Evolution of Reefs

R.A. WOOD

Introduction

In principle, any sessile marine organism can form a reef; indeed, the geological record shows that many different microbial, algal, and metazoan communities have formed reefs over the last 3.5 billion years (Fig. 1.3.3.1) (Fagerstrom 1987). Most of these communities, particularly those from the Palaeozoic, grew under ecological and environmental controls profoundly different from those that govern the functioning of modern coral reefs. Not only has the global distribution of reefs varied considerably through geological time—determined largely by fluctuating global sea level, and latitudinal gradients of temperature and calcium carbonate saturation—but more importantly the trophic demands of reef building organisms have changed, as has the degree of biological disturbance faced by immobile biota occupying shallow marine environments.

Reefs are discrete carbonate structures constructed by organic components that develop topographic relief upon the sea floor. Many direct and indirect biological processes promote the necessary high rates of *in situ* carbonate production to form a reef, including the activities of microbial communities, the aggregation of skeletal organisms, and the precipitation of inorganic cements within cavernous reef frameworks. An understanding of how reef-building organisms have responded to the changing demands of a sessile lifestyle, the mechanisms responsible for their aggregating behaviour, and how extrinsic physicochemical factors control carbonate production, are therefore all fundamental to the study of reef evolution.

The distinctive character of Palaeozoic reefs

Although some Palaeozoic reefs achieved rates of accretion similar to that shown by modern coral reefs (e.g. 3–4 mm/year for the Permian Capitan Reef of Texas and New Mexico), both the community structure and relative contributions of inorganic and organic carbonate were often profoundly different. Palaeozoic reefs appear to have grown in the absence of photosymbiosis and, in some examples, much of the preservable biodiversity was housed within cryptic communities. Moreover, reef construction by relatively fragile organisms was made possible by the absence of widespread bioerosion, and by rapid rates of early lithification that resulted from both microbial activity and inorganic cementation processes.

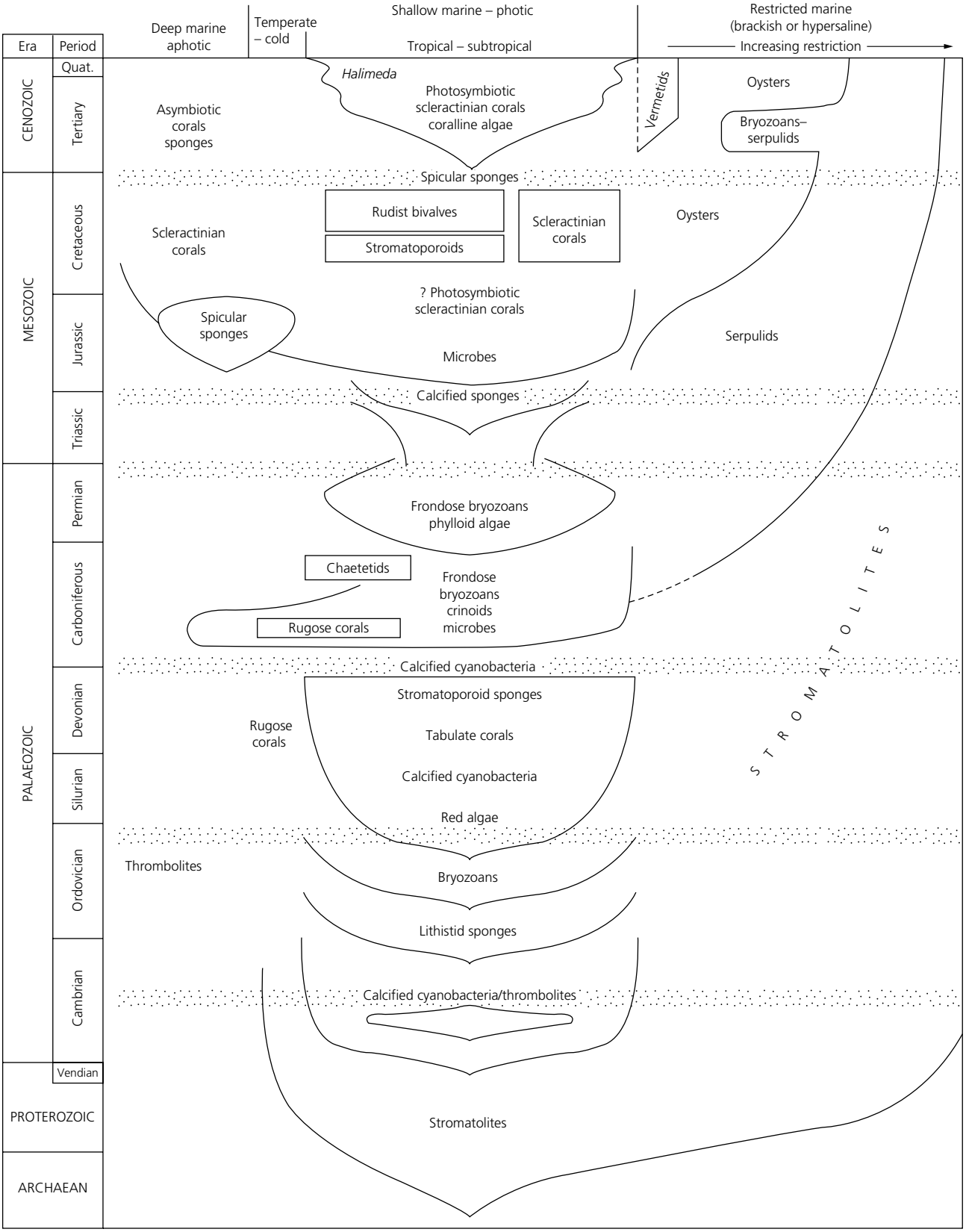

Fig. 1.3.3.1 A succession of many different organisms have built reefs through geological history, with the incumbency of many terminating during mass extinction events (stippled areas). (From Wood 1999.)

Stromatactis is a common but enigmatic structure found within many Palaeozoic reefs, consisting of cement-filled laminar voids within fine-grained carbonate, with either flat or undulose lower surfaces and irregular or digitate upper surfaces. Even though stromatactis may have more than one origin, it is strangely unknown from reefs younger than the Permian. However, the absence of stromatactis in non-reef, micritic Palaeozoic carbonates does not support an entirely non-biological origin, and the common presence of geopetal sediments and fibrous cement infill mitigates against formation entirely by processes involving replacement or dissolution. It is likely that many stromatactis structures will prove to have a reef framework origin, forming as a result of the growth of inconspicuous reef-building organisms or microbially induced structures.

The complexity of communities

Suitable substrates for colonization by benthic organisms have always been a limited resource, and it is now clear that habitat selection for small refuges was in operation as soon as open frameworks developed, some 1.9 billion years ago. From this time onwards, reef biotas have been differentiated into distinctive open surface and cryptic communities (Wood 1999).

Some of the earliest weakly calcified metazoans known from the terminal Neoproterozoic (e.g. *Cloudina*) (see Section 1.2.2) were sessile, gregarious, and probably heterotrophic organisms that were capable of forming limited topographic relief. Borings have also been recorded from this time (although probable sponge borings and silt-sized microspar grains resembling 'chips' from clionid-type sponges are first known from the Lower Cambrian), and a deposit-feeding fauna associated with reef cavities had developed by the earliest Cambrian (Zhuravlev and Wood 1995).

The earliest skeletal metazoan reefs appear at the base of the Tommotian, where it is exposed on the Aldan River, Siberia. These were already ecologically complex, with a framework of branching archaeocyath sponges, a cryptic biota of small archaeocyaths and calcified cyanobacteria, and an associated fauna of diverse small shelly fossils. With the widespread appearance of new groups of sessile, calcified organisms inferred to have been suspension- or filter-feeders, metazoan reef communities became established globally by the mid-Early Cambrian. This biota produced one of the most diverse and ecologically complex reef ecosystems known from the Palaeozoic (Fig. 1.3.3.2).

The importance of microbial communities

Microbialites are calcareous organosedimentary deposits that form by the interaction of benthic microbial communities with detrital or chemical sediments. Although the recognition of microbialites in the geological record is problematic and controversial, presumed microbialites are now recognized to be both common primary framebuilders and secondary encrusters within many Palaeozoic reefs: indeed, it is probable that they are more important than currently recognized (Pratt 1995; Webb 1996). Ancient reefs that consist of significant amounts of cement and putative microbialite, such as the celebrated Late Devonian Canning Basin reefs, Western Australia, and the Permian Capitan Reef, nonetheless formed substantial topographic barriers that separated deep basins from shallow lagoons behind. These two sources of carbonate can alone account for up to 75% of the reef rock volume (see Fig. 1.3.3.3).

Lower Carboniferous Waulsortian mounds—distinctive steep-sided reefs characterized by a core facies containing many generations of micrite, complex micrite-supported cavity systems infilled by marine cements including stromatactis, and fenestrate bryozoans—are also recognized to have formed under a stabilizing biological control. Most authors now agree that diverse and complex microbial processes were important in Waulsortian reef formation, whilst the contribution of skeletal organisms was variable and probably relates to differences in local depositional setting and opportunistic colonization. Encrusting, often cryptic stromatolites and thrombolites, and occasional putative cyanobacterial colonies, offer direct evidence of microbial activity, and the encrustation and boring of microbialite by invertebrates confirms both the primary origin and early lithification of this carbonate (Webb 1996).

Many modern microbialites appear to form only in environments where the growth of potential competitors for substrate space is excluded, and where oceanographic conditions create a water chemistry favourable for carbonate precipitation. The temporal distribution of microbialites over geological time scales may therefore be controlled by physicochemical factors, including the saturation state of sea water driven by changes in pCO_2 or Ca/Mg ratios, or global temperature distribution (Webb 1996). It has been suggested that the decline in abundance of reefal microbialite after the Jurassic resulted from the relatively reduced saturation state of sea water. This may have lowered supersaturation levels below a threshold for abundant microbialite formation, thereby restricting microbialite formation to cryptic reef habitats where abnormal chemistries can develop. Such a scenario might also be related to the disappearance of stromatactis at the end of the Palaeozoic.

The rapidity of early lithification

Many Palaeozoic reefs are characterized by large

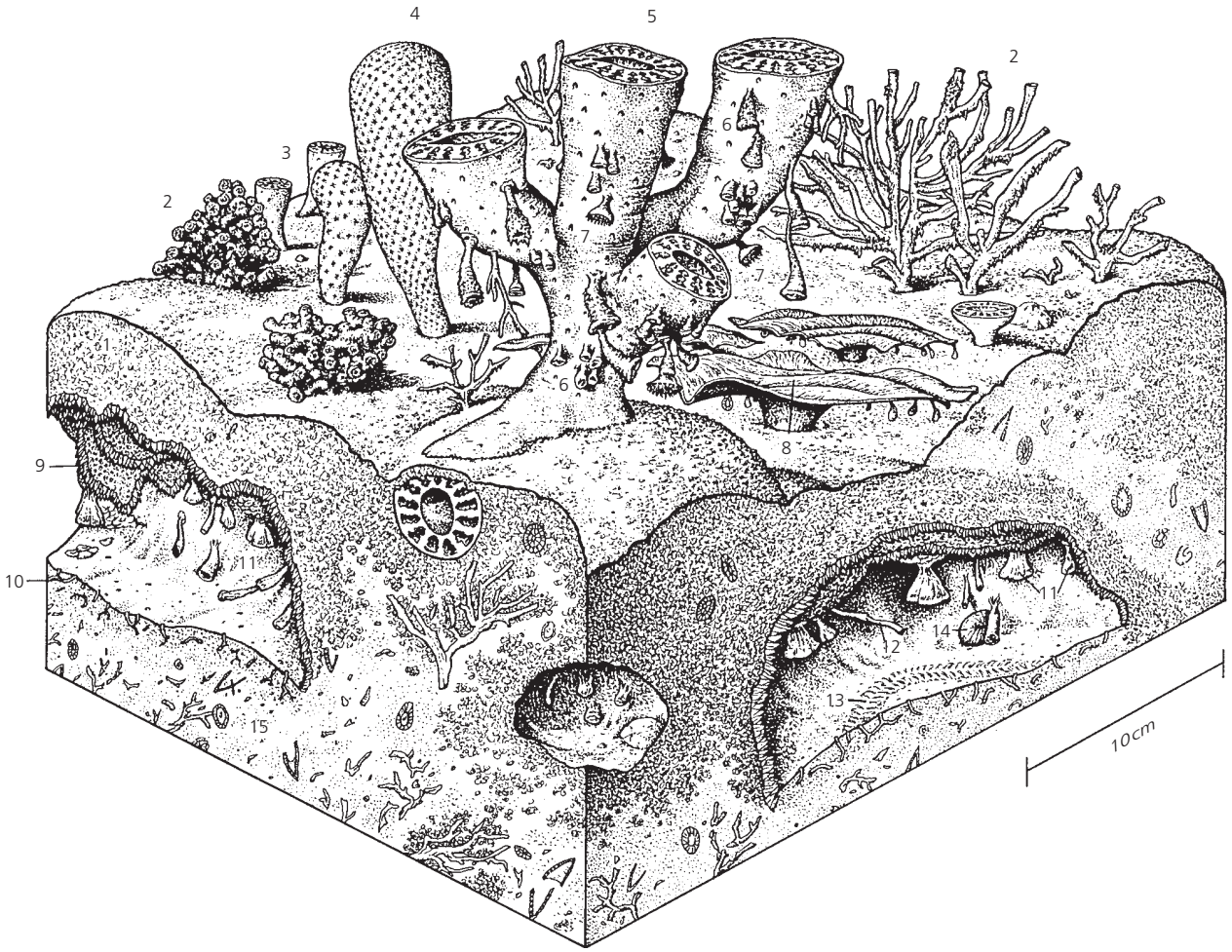

Fig. 1.3.3.2 Reconstruction of a Lower Cambrian reef community. 1, *Renalcis* (calcified cyanobacterium); 2, branching archaeocyath sponges; 3, solitary cup-shaped archaeocyath sponges; 4, chancelloriid; 5, radiocyath (?sponge); 6, small, solitary archaeocyath sponges; 7, cryptic 'coralomorphs'; 8, *Okulitchicyathus* (archaeocyath sponge); 9, early fibrous cement forming within crypts; 10, microburrows (traces of a deposit-feeder) within geopetal sediment; 11, cryptic archaeocyaths and coralomorphs; 12, cryptic cribricyaths (problematic, attached skeletal tubes); 13, trilobite trackway; 14, cement botryoid; 15, sediment with skeletal debris. (From Wood 1999.)

amounts of early marine cement. The importance of early cementation in reef formation on Palaeozoic rimmed shelves is manifest by the numerous, huge reef talus blocks commonly incorporated into fore-reef strata and basin debris flows, and the extensive development of neptunian dykes (vertical fissures often filled with marine sediment and cement) and other fractures subparallel to reef fronts. The abundance of early cements in Palaeozoic reefs compared to modern coral reefs reflects the substantial size and persistence of framework cavities in the absence of bioerosion, and is also suggestive of a poorly understood post-Palaeozoic change in the carbonate chemistry of sea water.

There is also limited evidence for very rapid rates of cement growth within many Palaeozoic reefs, shown by the fact that some cryptic organisms abut against, and become distorted by, cavity cements (Zhuravlev and Wood 1995). This would suggest the operation of important feedback mechanisms for reef formation in the Palaeozoic which have yet to be explored.

Major events in the evolution of Palaeozoic reef communities

The development of modularity

Notwithstanding the great diversity of invertebrates that have contributed to reef-building over the course of the Phanerozoic, there appears to be a limited number of functional organizations that have evolved repeatedly and independently, suggesting that variations in life history as expressed by growth form have always been

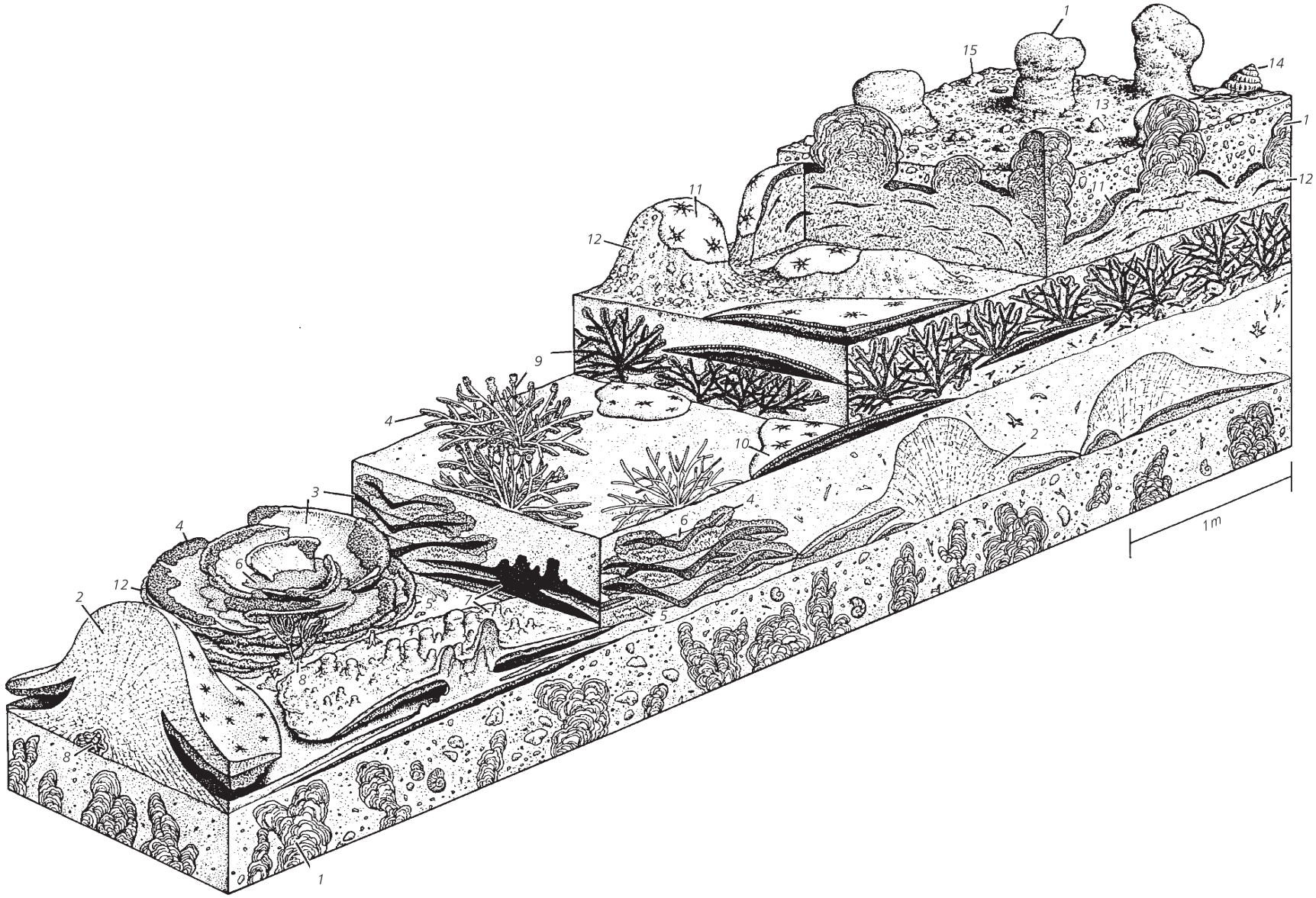

Fig. 1.3.3.3 Reconstruction of an Upper Devonian back-reef community, Canning Basin, Western Australia. Back-reef sediments show distinctive shallowing-upwards cycles from left to right, which are interpreted as the lateral zonation of four communities. 1, stromatolites; 2, domal stromatoporoid (*Actinostroma*); 3, inferred whorl-forming foliaceous stromatoporoids (?*Actinostroma* sp.); 4, calcified cyanobacterium (*Shuguria*); 5, fibrous cement; 6, geopetal sediment infill; 7, platy stromatoporoid; 8, crinoids; 9, branching stromatoporoid (*Stachyodes* sp.); 10, laminar stromatoporoid; 11, encrusting stromatoporoid (?*Clathrocoilona spissa*); 12, microbialite; 13, coarse clastic sediment; 14, gastropods; 15, oncolites. (From Wood 1999.)

important. Indeed, the processes controlling the distribution of ancient reef organisms appear to have been remarkably similar to those observed today (Jackson and McKinney 1991), as organisms with either densely aggregating growth or modular organizations have always been the most successful at acquiring necessary substrate.

Acquisition of a modular habit imparts many advantages to a reef-building organism, including the potential for unlimited growth and attainment of large body size, impressive powers of regeneration from partial mortality, and high fecundity. Not surprisingly, statistically significant increases in the proportion of forms with a modular organization is a widespread phenomenon in the history of many groups of reef-builders, including archaeocyath sponges, bryozoans, and corals. All these trends are polyphyletic, suggesting that there is a general premium on improving physiological interaction between modules regardless of taxonomic affinity (Jackson and McKinney 1991). While solitary and weakly integrated organizations were dominant within reef communities during the Cambrian and Lower Ordovician, encrusting skeletal invertebrates had become common by the mid-Ordovician, and by the mid-Devonian metazoan reef-builders had achieved a tremendous variety of modular morphologies, with individuals/colonies that could reach up to 5 m in diameter (Fig. 1.3.3.3) and with demonstrably impressive powers of regeneration. This resulted in the development of highly cavernous and tiered reef structures.

The reef landscape changed greatly during the course of the Phanerozoic. The majority of Palaeozoic reef metazoans lacked the means to gain secure and permanent attachment to a hard substrate, such that it is difficult to envisage such organisms living in the highly turbulent, surf-zone that reef corals and coralline algae occupy today. During the Palaeozoic, tropical shallow level bottoms often supported enormous populations of small erect bryozoans and stromatoporoid sponges: habitats which in the Recent show no apparent open surface community, only a diverse burrowing one. This disappearance might be explained by the Mesozoic marine revolution (see Section 1.4.1), which involved the dramatic rise of organisms with the ability to burrow deeply and to bore, gouge, or scrape: the armament which had provided ample protection against predators in the Palaeozoic had proved inadequate by the Cretaceous.

The role of mass extinctions

Although a succession of different ecosystems has formed reefs during Earth's history, the 'incumbency' of many of these long-lived ecosystems has been terminated by mass extinctions. Palaeozoic reef biotas suffered four major mass extinctions: at the end of the Early Cambrian, the end-Ordovician (see Section 2.4.2), the Late Devonian (see Section 2.4.3), and the end-Permian (see Section 2.4.4). Although not all mass extinction events preferentially affected tropical areas, there are data to suggest that all carbonate platform biotas are more susceptible to environmental perturbation than those occupying other habitats at low latitudes. Notwithstanding the dramatic reduction in the diversity of reef-associated metazoans, calcified cyanobacterial and microbial communities still persisted to build reefs where carbonate platforms continued to form, perhaps due to their reduced sensitivity to the sustained reductions in primary productivity often associated with mass extinction events. Indeed many reef ecosystems appear to be remarkably resilient to mass extinction events, which seem to have had little effect on the appearance of new reef biotas. While many mass extinctions are associated with a change to a new biota, the extinction event appears to have only accelerated changes that were often already apparent and advanced.

References

Fagerstrom, J.A. (1987) *The evolution of reef communities*. John Wiley and Sons, New York.

Jackson, J.B.C. and McKinney, F.K. (1991) Ecological processes and progressive macroevolution of marine clonal benthos. In: R.M. Ross and W.D. Allmon, eds. *Causes of evolution*, pp. 173–209. University of Chicago Press, Chicago.

Pratt, B.R. (1995) The origin, biota and evolution of deep-water mud-mounds. In: C.L.V. Monty, D.W.J. Bosence, P.H. Bridges and B.R. Pratt, eds. *Carbonate mud mounds: their origin and evolution*, pp. 49–123. International Association of Sedimentologists, Special Publication no. 23. Blackwell Science, Oxford.

Webb, G.E. (1996) Was Phanerozoic reef history controlled by the distribution of non-enzymatically secreted reef carbonates (microbial carbonate and biologically induced cement)? *Sedimentology* **43**, 947–971.

Wood, R.A. (1999) *Reef evolution*. Oxford University Press, Oxford.

Zhuravlev, A.Yu. and Wood, R.A. (1995) Lower Cambrian reefal cryptic communities. *Palaeontology* **38**, 443–470.

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1.3.4 Early Land Plants

D. EDWARDS

Introduction

Land plants encounter problems relating to water stress, uptake, and transport, and to aerial dispersal. Survival is associated with three major strategies: (1) drought avoidance via opportunism and ephemeral life cycles completed under favourable conditions; (2) desiccation tolerance in the vegetative state involving the capacity of cytoplasm to rehydrate and then function normally (poikilohydry); and (3) maintenance of an internally hydrated environment by biochemical and anatomical modifications (homoiohydry).

Extant land vegetation includes representatives of cyanobacteria, algae, bryophytes, and tracheophytes. The last are usually considered most successful in exploitation of terrestrial environments and are homoiohydric—possessing xylem (with lignin) for water transport, a waxy cuticle (cutin) for reducing evaporation, and stomata and an intercellular space system for gaseous transport. The poikilohydric lifestyle of many cyanobacteria, algae, and bryophytes is of particular significance in the colonization of unstable, ephemeral and highly stressed environments, and hence would have been important in pioneering land plants.

The *preservation potential* of land plants is linked to these strategies in that cutin and lignin are durable and may persist, albeit modified, in fossils, but in poikilohydric forms the only parts which might be expected to be fossilized are resting stages and diaspores. The latter, impregnated with sporopollenin, a complex fatty polymer, also characterize tracheophytes. Thus although there is no direct record of terrestrial cyanobacteria and algae in the early Palaeozoic, it seems likely that they were present. High ultraviolet (UV) radiation correlated with low atmospheric oxygen may have limited their distribution. Indeed it has been postulated that lignin evolved from precursors involved in UV absorbance, and that cutin and sporopollenin initially had a similar role.

Regarding higher plants, attempts to demonstrate tracheids of megafossils, thus providing unequivocal evidence for land vegetation, have traditionally dominated research. More recently the affinities of Ordovician and Silurian microfossils have been rigorously appraised in the search for alternative pioneering colonizers.

Terrestrialization

The first records and ranges of all fossils thought relevant to terrestrialization are documented in Fig. 1.3.4.1.

1 *Obligate permanent tetrads* are so named because they do not split into four spores (monads) on dispersal. They possess durable, smooth, unornamented walls, thought to be impregnated with sporopollenin (although this has not been chemically proven). Some are enclosed within a smooth or ornamented resilient envelope ('membrane'). Both forms are common in Llanvirn to late Llandovery assemblages when the first true triradiate monads appear. Thereafter tetrads become less common and occur only rarely in the Lower Devonian. Older monads with irregular triangular tears probably represent torn apart tetrads. Tetrads are thought to derive from land plants because of their resilient walls and production in fours (a meiotic configuration). As comparable tetrahedral tetrads occur in certain liverworts (e.g. *Riccia*, *Sphaerocarpos*), they are believed to derive from poikilohydric plants with bryophyte physiology and life histories (Gray 1985). The earliest *in situ* examples occur in terminal sporangia on smooth bifurcating axes (not a characteristic of extant bryophyte sporophytes). The axes lack the anatomical data enabling placement within either bryophytes or tracheophytes. Envelope-enclosed *obligate dyads* (**2**) have similar ranges to tetrads and were probably of similar derivation.

2 *Dyads*. Naked and enveloped permanent dyads, assumed to represent a departure from normal meiosis in that separation occurred after the first division, occur abundantly from Llanvirn to lower Llandovery when enveloped permanent dyads decrease dramatically.

3 *Hilate monads* (i.e. lacking a trilete mark in a normal circular contact face) appear in the Llandovery and then proliferate in numbers and diversity into the lower Devonian. The upper ranges of the three morphotypes are unclear.

Sculpturing of the exospore wall is first recorded in the Homerian. Hilate monads and permanent dyads occur in *Salopella*-shaped sporangia in the Lower Devonian, some terminating branching axes. Anatomical evidence for affinity is lacking, but transmission electron micrographs of dispersed naked dyads *Dyadospora murusattenusata* show lamellae in the wall that are characteristic of liverwort spores, although not exclusively so (Taylor 1997). *In situ* examples of dyads and hilate monads have homogeneous walls. Dispersed examples show greater ultrastructural diversity.

4, 5 *Monads with triradiate marks*. The earliest monads are smooth-walled, usually with equatorial thickening, e.g. *Ambitisporites* (which is later recorded in Přídolí *Cooksonia pertoni* sporangia). Sculptured monads occur

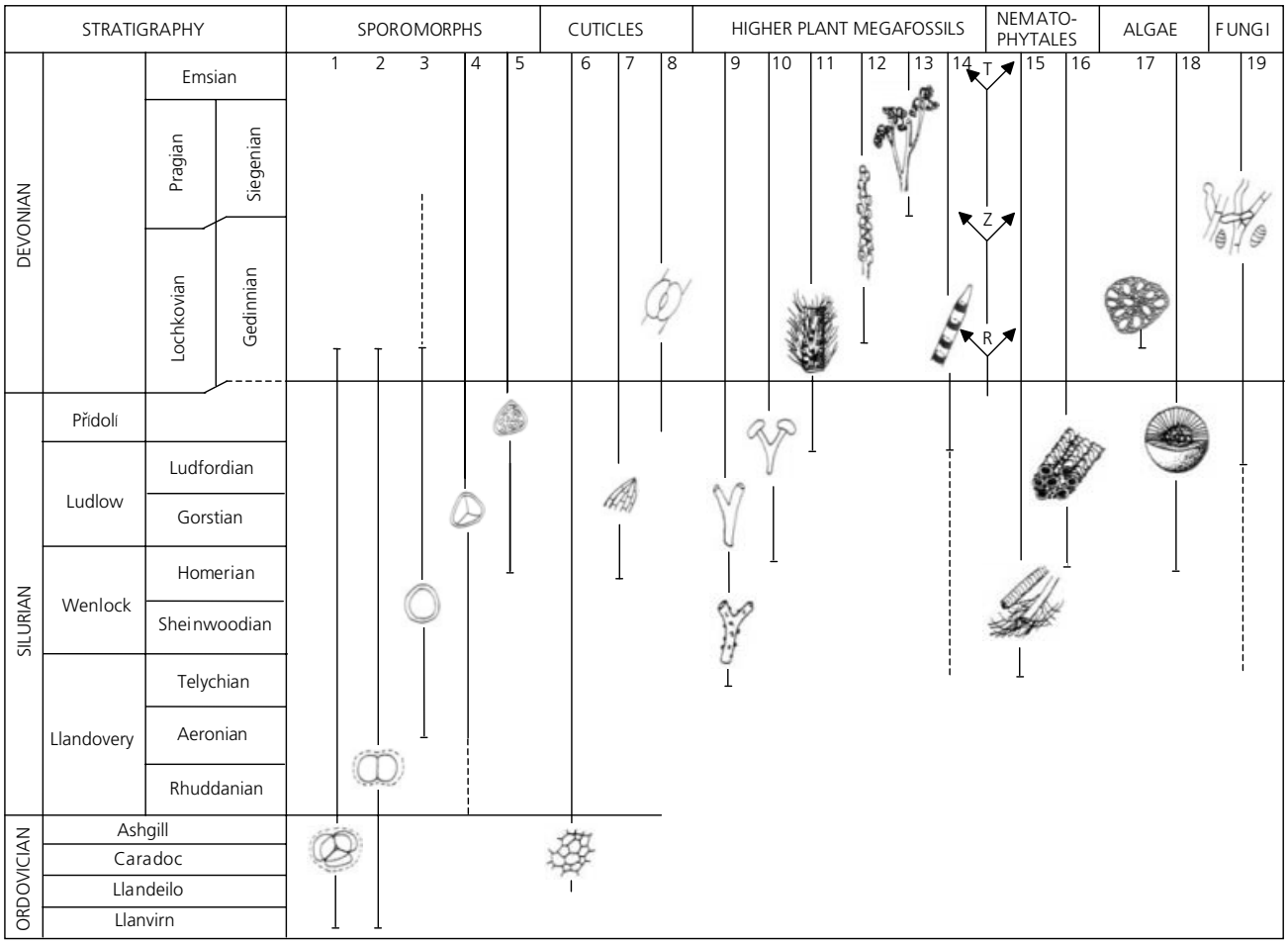

Fig. 1.3.4.1 First appearances and stratigraphic ranges of microfossils and megafossils relating to the colonization of land by plants. R, Z, and T refer to initial major radiations of the vascular plant subdivisions Rhyniophytina, Zosterophyllophytina, and Trimerophytina, respectively. For more complete explanation of 1–19, see text.

continuously from the Homerian, showing rapid diversification and proliferation in the Ludlow and Přídolí. The *in situ* examples, recorded from the Přídolí onwards (Edwards and Richardson 1996), demonstrate that spore characteristics can be diagnostic, e.g. those with well-defined contact faces (retusoid) characterize the zosterophylls, and with equatorial thickening (crassitate), *Cooksonia pertoni*. Greatest diversity is noted in small axial plants with terminal sporangia, termed rhyniophytoid because they reveal no anatomical detail for more precise assignment.

6 '*Nematothallus*'. Associated with the earliest sporomorphs are small cuticular fragments with one smooth surface, and the other a raised isodiametric reticulate pattern representing the outer cells of the tissue below. Unlike tracheophyte cuticle, they lack stomata and are usually imperforate. Recent analysis using pyrolysis-gas chromatography/mass spectrometry (Py-GC/MS) indicates a different chemical composition from that of coeval tracheophyte cuticles. In some instances they cover *Nematothallus*, a thalloid plant composed of tubes placed in the Nematophytales (**15**, **16**), a taxon for plants neither algal nor higher plant (Lang 1937).

Whether all durable spores derived from land plants remains in doubt, but this is not so for cuticles. Because they are imperforate, they may have been more permeable to gases and water than in tracheophytes, and hence their function in *Nematothallus* might have been different, e.g. primarily as UV screens, facilitating runoff, or in defence. It is unlikely that they belonged to the tetrad producers (**10**) because, although their first records are coincident, cuticles persist into the Emsian and are sometimes quite common constituents of Lower Devonian assemblages.

7, 8 *Higher plant cuticles*. Homerian fragments with larger, more strongly demarcated and aligned cells are interpreted as sporangial from comparison with dispersed and *in situ* Lochkovian examples from rhynio-

phytoid and dyad producers. Astomatous cuticles deriving from sterile axes occur in the northern hemisphere Ludlow. The earliest *direct* evidence for stomata (with two guard cells) comes from sterile and fertile axes in the Přídolí, with examples on *Cooksonia* and *Zosterophyllum* in the Early Devonian. However, since stomata are evident on Canadian Emsian *Baragwanathia abitibiense* they were probably also present on the earlier Australian Ludlow *B. longifolia*, where cells are not preserved.

9 *Sterile axes*. Those with dichotomous branching and peripheral support tissues (stereome), the earliest being Llandovery *Eohostimella*, are thought to derive from erect land plants. Late Silurian and Early Devonian examples (e.g. *Hostinella*) possess a central strand of tracheids (**14**), but whether or not pre-Ludlow representatives were vascular is unknown. Some may derive from plants of small stature in which tracheids had not yet evolved; others may possess conducting tissues of bryophytic nature (e.g. the Lower Devonian *Aglaophyton major* exhibits many homoiohydric characters and would be assigned to the Tracheophyta but for the moss-like conducting tissues). Particularly puzzling are some extensive pinnately branching axial systems named *Pinnatiramosus* with unequivocal xylem elements showing bordered pits, recorded from the marine Llandovery, Guilin, China. In size, morphology, and sophistication of anatomy, the fossils are closest to the roots of younger Palaeozoic spermatophytes. They are certainly more complex than those in the earliest lycophytes, of which *Baragwanathia* is first recorded in the Australian Ludlow. Its sterile leafy shoots are morphologically similar to Lower Devonian examples that from morphology, anatomy, and sporangia are herbaceous lycophytes.

10–13 *Fertile tracheophytes*. Wenlock *Cooksonia* (**10**) is generally accepted as the earliest erect pteridophyte-like plant. Reservations as to its affinity stem from absence of anatomy. Spores occur in the Přídolí, and stomata, stereome, and tracheids in Lochkovian examples. Other taxa (e.g. *Salopella*, *Steganotheca*) are usually assigned to the Rhyniophytina on general morphological similarity to later examples (e.g. *Rhynia gwynne-vaughanii*) but are better called 'rhyniophytoid' to emphasize our ignorance. A major radiation is recorded in the early Lochkovian: they then became insignificant constituents of land vegetation (Edwards and Davies 1990).

Zosterophyllum myretonianum (**12**) is the earliest fertile member of the Zosterophyllophytina: records of its characteristic branching (K- and H-shaped) occur in sterile Přídolí axes. The first major zosterophyll radiation is recorded in the late Lochkovian of South Wales. *Dawsonites* sp. (**13**), a fragment of a fertile truss of *Psilophyton* in the South Wales Pragian, marks the beginnings of the Trimerophytina, the Ludlow Australian record being less convincing. The trimerophytes diversified rapidly in the Emsian and are considered ancestral to ferns *sensu lato*, progymnosperms, and sphenopsids.

15 *Microfossils of tubular organization* are recorded as isolated tubes or wefts, from the Telychian into the Lower Devonian (Gensel *et al.* 1990). The most conspicuous tubes are internally sporadically thickened ('banded'), thus broadly resembling tracheids, but there is no evidence that they were lignified. The source plants are problematic: the banded tubes occur with smaller tubes in *Nematothallus* (Lang 1937) and have been found in plants with organization otherwise typical of *Prototaxites* (**16**). While possibly the remnants of cells in the sporangial wall of bryophytes, recent records of banded tubes attached to sporangial surfaces and axes, and their penetration between tissues, suggest a pathogenic or saprotrophic lifestyle. The habitats of such organisms, be they freshwater or terrestrial, remain as conjectural as their affinities. In that some smooth tubes have been recorded attached, rather than just adpressed to cuticles of *Nematothallus* (**6**) type, they may well derive from land plants. Further isolated examples include tubes with smooth, thick or thin walls, or filaments (occasionally branched) composed of elongate, narrow cells. The latter frequently occur in monotypic wefts or may be associated with wider smooth or banded tubes or even spores.

16 *Prototaxites* (Wenlock–Upper Devonian) is usually cited as a land plant because it occurs with tracheophyte assemblages in freshwater sediments. Its organization, in which narrow filaments surround wider, smooth tubes, is unique and hence, in the absence of reproductive organs, its affinities, possibly algal or fungal, remain unknown.

17 *Parka*, best known from the Scottish Lochkovian, a possible epiphyte in lacustrine habitats, may have some relevance to the ancestry of higher plants in that it has been compared with the charophycean *Coleochaete*, although the latter lacks the cavities with numerous alete spores found in *Parka*. Among the green algae, *Coleochaete*, with its parenchymatous organization, and protection, nutrition, and prolonged retention of the zygote, possesses the greatest number of advanced features in the Charophyceae; comparative biochemical and ultrastructural studies suggest that the Charophyceae show closest similarities with bryophytes and tracheophytes (Kenrick and Crane 1997).

18 *Pachytheca* is exceedingly common in certain marginal fluviatile and lacustrine Lower Devonian facies. Its frequent association with *Prototaxites* has led to the suggestion that it was involved in its vegetative reproduction. However, the fossils suggest that the organism comprised a sphere of a mucilage-like substance in which filaments of cyanobacterial dimensions were embedded. Its habitat is interpreted as freshwater, possibly littoral lacustrine.

19 *Fungi*. Although not considered plants, fungi are

included here because it has been suggested that initial terrestrialization was possible only after the development of a symbiotic association between a semiaquatic green alga and an aquatic oomycete fungus, and that in the colonization of nutrient-poor environments, the fungus would have exploited large volumes of substrate for minerals (cf. mycorrhiza today). Mycorrhiza occur in Pragian Rhynie chert *Aglaophyton* axes as hyphae within tissues and as resting spores, although the latter may be connected with saprotrophism (i.e. decomposition of dead organisms). Parasitic chytrids (simple, aquatic fungi) and the earliest lichen are also recorded in the Rhynie chert. Further evidence for terrestrial fungi are the ascomycetes (hyphae, probable conidia, and ascospores) from the Ludlow of Gotland, and similar, but more poorly preserved, material from the late Llandovery.

Terrestrial vegetation

It is postulated that moist land surfaces in the early Palaeozoic would have been coated with a green scum, perhaps initially of cyanobacteria and eubacteria, later joined by filamentous and unicellular algae (Gray 1993). Such an encrusting layer would have both physically stabilized and chemically broken down the substrate, releasing nutrients and, in stable environments, resulted in limited build-up of humus. From the Llanvirn onwards microfossils morphologically convergent with those from extant embryophytes suggest a novel vegetation comprising a 'turf' of small plants with bryophyte life-style that produced spores at the tips of unbranched or bifurcating leafless axes; aerial dispersal indicates the attainment of some stature. The appearance of *Ambitisporites* in the Llandovery heralded a new phase—that of pteridophyte-like plants with axial organization, again forming a 'turf' a few centimetres high. The larger size permitted by homoiohydry, the concomitant maintenance of turgor and hence a hydrostatic skeleton conferred potential superiority over poikilohydric forms in terms of wind dispersal of propagules and in shading, thus limiting the productivity of smaller forms. Throughout the Late Silurian there was an increase in diameter and length of fragments suggestive of larger axial plants; sprawling *Baragwanathia* probably formed thickets. Lower Devonian assemblages suggest that many of the tracheophytes grew in monotypic stands, extensive cover resulting from prolonged rhizomatous activity. Such plants would have provided mutual support—some Emsian trimerophytes were over 1 m tall. Truly arborescent plants with secondary wood appeared later in the Middle Devonian (see Section 3.4.5). As to habitats, the best direct evidence comes from the Rhynie chert (see Section 3.4.5), but as all these early embryophytes were homosporous (i.e. with spores of one size), the free-living gametophyte would have required moist conditions for reproduction. With regard to the route of terrestrialization for higher plants, physiological considerations support transmigration from fresh water on to land.

Much broader issues relating to these phases of terrestrialization include their impact on Palaeozoic atmospheres and climates. Thus in Berner's (1997) model of the concentration of carbon dioxide in the atmosphere during the Phanerozoic, the proliferation and eventual decomposition of tracheophytes throughout the Devonian is postulated as having contributed to a major drawdown of atmospheric CO_2 via chemical weathering of rocks, when Ca/Mg silicate minerals would have been weathered and subsequently precipitated in oceans as carbonates. The quantitative role of pretracheophytes in such weathering processes during the early Palaeozoic remains uncertain.

References

Berner, R.A. (1997) The rise of plants and their effect on weathering and atmospheric CO_2. *Science* **276**, 544–546.

Edwards, D. and Davies, M.S. (1990) Interpretations of early land plant radiations: 'facile adaptationist guesswork' or reasoned speculation? In: P.D. Taylor and G.P. Larwood, eds. *Major evolutionary radiations*, pp. 351–376. Systematics Association, Special Volume no. 42. Clarendon Press, Oxford.

Edwards, D. and Richardson, J.B. (1996) Review of *in situ* spores in early land plants. In: J. Jansonius and D.C. McGregor, eds. *Palynology: principles and applications*, Vol. 1, *Principles.* American Association of Stratigraphic Palynologists Foundation, pp. 391–407. Publishers Press, Salt Lake City, Utah.

Gensel, P.G., Johnson, N.G. and Strother, P.K. (1990) Early land plant debris (Hooker's 'waifs and strays'?). *Palaios* **5**, 520–547.

Gray, J. (1985) The microfossil record of early land plants: advances in understanding of early terrestrialization, 1970–1984. *Philosophical Transactions of the Royal Society of London B* **309**, 167–195.

Gray, J. (1993) Major Paleozoic land plant evolutionary bioevents. *Palaeogeography, Palaeoclimatology, Palaeoecology* **104**, 153–169.

Kenrick, P. and Crane, P.R. (1997) *The origin and early diversification of land plants: a cladistic survey*. Smithsonian Institution Press, Washington and London.

Lang, W.H. (1937) On the plant-remains from the Downtonian of England and Wales. *Philosophical Transactions of the Royal Society of London B* **227**, 245–291.

Taylor, W.A. (1997) Ultrastructure of lower Paleozoic dyads from southern Ohio II: *Dyadospora murusattenuata*, functional and evolutionary considerations. *Review of Palaeobotany and Palynology* **97**, 1–8.

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1.3.5 Afforestation—the First Forests

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Introduction

Although terrestrial ecosystems had begun by the Middle Ordovician (Retallack 1990; Beerbower *et al.* 1992), the typical growth plan of plants—axis construction via apical meristems (growing tips)—was uncommon before the Middle Silurian. The first plants were less than 0.5 m tall and simply constructed of progressively diminishing forked axes. Robust plant architectures are uncommon until near the end of the Early Devonian (Pragian–Emsian) (Fig. 1.3.5.1a) and result from more complex branching patterns of apical meristems. Main axis/overtopped-lateral-branch designs, and tissue patterns capable of meeting increased support and conductance requirements, became common in several plant groups, such as trimerophytes, cladoxylopsid ferns, and cormose lycopsids (whose members reached 2–3 m high) (Fig. 1.3.5.1a,b).

Plant size increased sufficiently by the early Middle Devonian (Eifelian) (Fig. 1.3.5.1b) so that 'trees' can be recognized, although they are small by modern standards (Chaloner and Sheerin 1979). More importantly, these trees became common and widespread as a result of root innovations that penetrated soils more deeply and stabilized floodplain habitats (Retallack 1990; Beerbower *et al.* 1992; Algeo and Scheckler 1998). The extent of terrestrial colonization, indicated by frequency, areal extent, and depth of palaeosols, and the abundance of macrofossil debris, dramatically surged as forest ecosystems became permanent additions to the landscape (Algeo and Scheckler 1998).

Trees radiated more or less simultaneously from three distinct lineages: woody aneurophyte progymnosperms and cladoxylopsid ferns, which are both trimerophyte allies, and cormose lycopsids (Fig. 1.3.5.1b). Each group persisted, expanded, and/or gave rise to new groups of tree-sized descendants throughout the Late Devonian and Early Carboniferous, but each used different 'styles' of growth, branching, and tissue design.

New Late Devonian groups include archaeopterid progymnosperms (the first truly large woody trees to form extensive forests), 'seed-fern' gymnosperm shrubs, giant reed-like calamite sphenopsid trees, additional but taller cormose lycopsid trees, a variety of woody vines (sphenophyll sphenopsids and cladoxylopsids), and sprawling rhizomatous zygopterid ferns (Fig. 1.3.5.1c). Further additions in the Early Carboniferous include forest and swamp trees, and shrubs of progymnosperm, gymnosperm, and stigmarian lycopsids. These components produced patchy vegetation characterized by monotypic-stand growth where many local habitats were filled by plants with clade-specific biological adaptations of rooting, growth architecture, or reproduction.

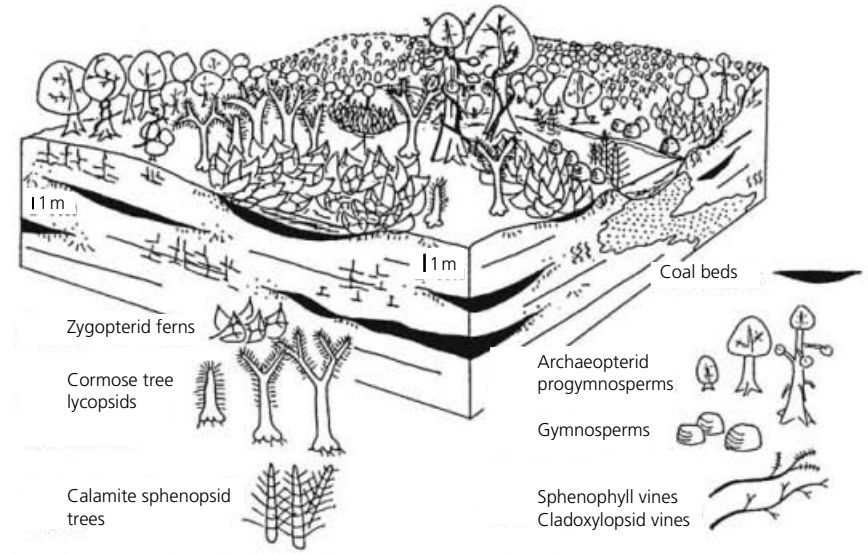
Mechanical/physiological properties of early trees

Progymnosperms and gymnosperms (lignophytes) used the innovations of bifacial (from both sides) vascular cambium (the growing layer producing wood cells inward and bark cells outward) and cork cambium (the growing layer repairing splits and wounds within bark) to produce thick woody trunks and branches (Beck 1988; Stewart and Rothwell 1993; Taylor and Taylor 1993). Wood and bark simultaneously accommodated the load bearing, fluid transport, and starch storage needs of perennially elongating and thickening trunks and limbs, and cork cambium formed a renewable outer protective surface.

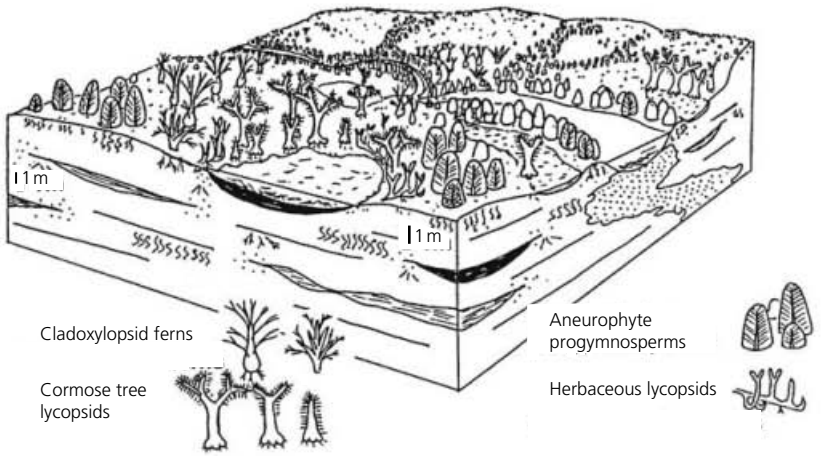
Aneurophyte progymnosperms and 'seed-fern' gymnosperms (Fig. 1.3.5.1b,c) were smaller shrub-like plants with less cambial growth, but they had pronounced outer cortex networks of interconnected fibre bundles, which made them flexible, yet stiff and wiry. Unequal apical branching produced highly branched trunks with successions of decreasing lateral branches (aneurophytes) or unbranched trunks with crowded megaphyllous leaves (seed-ferns). Such growth 'styles' produced short-lived trees with predictable final shapes and only limited abilities to regrow following injury. They occurred typically in dense stands, where branch/leaf contact with adjacent shrubs helped to support the grove.

Late Devonian *Archaeopteris* trees (10–30 m tall progymnosperms with vigorous woody growth) (Fig. 1.3.5.1c) produced many large lateral branches from later-formed buds (similar to modern gymnosperms) that enabled them to produce new branches following injury or crown senescence. Anchorage by vigorous, perennial, and highly branched root systems made these lignophytes sturdy forest components. Some *Archaeopteris* had buttressed trunk bases where the main roots joined. Extensive, deeply rooted palaeosols show that these woody trees formed streamside gallery forests and dense forest patches on coastal plains (Fig. 1.3.5.1c) (Retallack 1990; Beerbower *et al.* 1992; Algeo and Scheckler 1998).

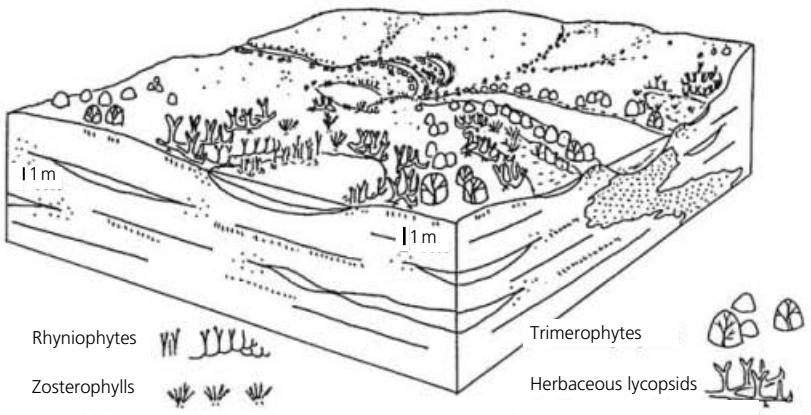
Cormose and stigmarian lycopsids (Fig. 1.3.5.1b,c) also had vascular cambium, but it was unifacial (growing layer produced wood only inward) and limited in both extent and duration. Little wood was produced, so that only a small xylem core supplied their fluid transport needs. Tree lycopsids had thick primary



(c) **Late Devonian (Famennian)**



(b) **Middle Devonian (Eifelian–Givetian)**



(a) **Early Devonian (Pragian–Emsian)**

Fig. 1.3.5.1 (a–c) Reconstructed Devonian landscapes. (Modified from Algeo and Scheckler 1998.)

cortex with vigorous periderm that produced thick 'secondary cortex' which provided both mechanical support and storage capacity. They are found in wetland deposits and had swollen trunk bases from which thick, hollow, unbranched (or once forked), and short (less than 1 m) 'stigmarian rootlets' emerged to penetrate wet muds or sands (Retallack 1990; Stewart and Rothwell 1993; Taylor and Taylor 1993). Unbranched young trunks were clothed by long thin leaves (Fig. 1.3.5.1b,c). Upon reaching certain heights or states of maturity, trunk apices forked equally (in Middle–Late Devonian taxa) or unequally (some Early Carboniferous taxa) to form small crowns of successively smaller lateral branches that interpenetrated in close stands (Fig. 1.3.5.1b,c). Crown branching is associated with the onset of reproduction. Although hardly woody by lignophyte standards, these lightweight, swollen-based, unbranched (or branched with small crowns) trunks, 5–20 m in height, were easily supported and anchored in wetland habitats. *In situ* stumps show that they were often closely spaced.

Cladoxylopsid trees (Fig. 1.3.5.1b) had thick much-branched trunks (2–3 m tall) with swollen bases from which tufts of branched roots emerged. Long (1–2 m) branches covered the trunk or formed a crown of digitate/forked branches that bore smaller forked, leaf-like branchlets. Internally, trunks and branches had many separate but vertically interconnected xylem strands that form the anatomical signature of this clade (Stewart and Rothwell 1993; Taylor and Taylor 1993). Pith is of loose, soft tissues, while cortex is mostly parenchymatous but may have an outer rind with clusters of tough sclereid cells; fibres are mostly absent. Cork cambium was absent, suggesting that axes of different widths were achieved by apical meristem growth (i.e. large axes had large growing tips). These were lightweight axes with high strength to weight ratios. The disposition of many separate xylem bundles resulted in some strands being under tension while those on the other side of an axis were load-bearing and under compression. Branches with this multistranded design were also rotationally flexible. Trunks were stiffer as a result of xylem augmentation (resembling cambium activity) of some bundles. Cladoxylopsid trees were ubiquitous but uncommon components of drier floodplain habitats. Other cladoxylopsids were flexible vines and climbers.

Reproduction of early trees

Although clonal vegetative propagation was common among Devonian herbaceous lycopsids, trimerophytes, and zygopterid ferns, most trees freely shed spores as their sole means of reproduction. Distance of spore dispersal relates to spore size (buoyancy), wind speed, and height of release. Two syndromes characterize the first trees: free-sporing homospory (where dispersed small spores germinate into free-living, potentially bisexual gametophytes) and free-sporing heterospory (where dispersed large or small spores germinate into female or male gametophytes, respectively, that are mostly confined to and dependent upon food reserves stored within each spore). The latter syndrome is temporally linked to emergence of tree-sized plants.

Heterospory may have been selected for as increased plant height made spore dispersal more effective (Chaloner and Sheerin 1979). This perhaps had a positive feedback in that taller plants had increased reproductive success (by farther dispersal or by regulating population biology via unisexual gametophytes). Competition for light is cited as the primary selection factor for increased plant height and crown spread; larger plants were better competitors for scarce light in increasingly crowded landscapes. Another possible feedback is greater leaf surface area for photosynthetic CO_2 capture, made necessary by rapid global atmospheric CO_2 drawdown in the Middle–Late Devonian (Berner 1997, 1998; Algeo and Scheckler 1998) that resulted from increased photosynthesis and production of thick chemically weathered soils. Regardless of which factors selected for tree size, nearly all Middle–Late Devonian large trees were heterosporous.

Early gymnosperms (mid-Famennian) exploited another type of heterospory where one functional megaspore (female) was retained inside its sporangium (ovule) while the microspores (pollen) were freely dispersed for potential capture by the tubular tips of female sporangia (pollination biology). Unique to seed plant heterospory is the parasitic nutrition of both female and male gametophytes that makes their growth independent of environmental water, sunlight, or fungal mutualism. The emergence of seed biology is linked to adaptations of early gymnosperms for pioneering dry habitats (Beerbower *et al.* 1992).

Devonian landscapes

Early Devonian

The expansion and diversification of plants in the Early Devonian (Fig. 1.3.5.1a) protected floodplains and soils from erosion, so that secondary succession (regrowth/replacement of taxa after disturbance) became dominant over primary succession (colonization of bare substrates and replacement of pioneer taxa as sites/soils matured). Bank-dwelling plants stabilized stream channels and promoted meandering rather than braided stream courses. These and floodplain dwellers served to delay and lessen the effects of devastating flash floods so that soil formation on interfluves was less frequently and less critically interrupted by sedimentation

or scour (Retallack 1990). As forests appeared in Middle–Late Devonian (Fig. 1.3.5.1b,c) they had an even greater impact (Algeo and Scheckler 1998).

Late Silurian and Early Devonian rhyniopsids and zosterophylls were small, rhizomatous plants that formed local monotypic patches by clonal growth. Bottoms of shallowly buried rhizomes or corms bore only tufts of rhizoids or short roots for anchorage and absorption. They utilized mainly surface water and were probably limited to habitats with nearly continuous moisture.

By mid–late Early Devonian (Pragian–Emsian), however, new plant architectures emerged. Tall main axes of trimerophytes bore overtopped lateral branches. Lycopsids had robust forked aerial axes covered by small leaves (Fig. 1.3.5.1a). Rhizomes of both groups produced sparse, small forked roots that penetrated shallow soils. Root penetration of floodplain deposits is absent or scarce before the Pragian, but is common thereafter. Subsurface water and dissolved soil nutrients were utilized so that slightly drier habitats could be colonized.

Middle Devonian

Trailing, herbaceous lycopsids often dominated local beds, with rhizomatous clones producing large monotypic patches. By the Givetian, however, tree-sized lycopsids with solitary, non-clonal growth were common (Fig. 1.3.5.1b).

Trimerophyte relatives also produced solitary trees, such as those of cladoxylopsid construction, and aneurophyte and archaeopterid progymnosperms. All had nonlaminated leaves or branchlets that allowed light penetration for understorey vegetation. Tiered ecosystems, that vertically stratified light and humidity, are linked to heterospory and they also promoted niche diversification of understorey plants. Stabilized floodplains developed local microclimates and distinctive soils that produced horizontally complex, patchy vegetation (Fig. 1.3.5.1b).

Late Devonian

Archaeopteris appeared in the early Late Devonian (Frasnian) and rapidly spread worldwide (Fig. 1.3.5.1c). All species except one had laminated leaves that made deeply shaded forests. *Archaeopteris* grew in well-drained to waterlogged soils and formed dense, streamside galleries, whereas drier interfluves supported other herbaceous or shrubby plants, such as cladoxylopsid shrubs/vines and trailing lycopsids (Retallack 1990; Beerbower *et al.* 1992). *Archaeopteris* tolerated many soil conditions (wet to seasonally dry) and formed extensive floodplain forests of only a few species (Beerbower *et al.* 1992; Algeo and Scheckler 1998). Most wetland habitats, however, were occupied by tree lycopsids or zygopterid ferns. Late Devonian riparian landscapes were thus marked by abrupt, small-scale, spatial heterogeneity (Fig. 1.3.5.1c).

Archaeopteris shed its leafy branches after one season of growth, possibly during a dry season. Deep litter accumulated in these forests and provided the innumerable branches preserved, during floods, in fluvial sediments. If the branches were shed throughout the year, then forest floors would have remained shady. However, if most leafy branches were shed during a dry season, then understorey vegetation had wide seasonal variation in light and humidity. Large amounts of fuel accumulated in *Archaeopteris* forests. Coupled with rising pO_2 as pCO_2 fell, fire became important for succession by Famennian times (Beerbower *et al.* 1992; Berner 1997, 1998; Algeo and Scheckler 1998).

Global impacts of forests

Forest expansion stabilized stream banks and floodplains and dramatically increased sediment retention time, so that more clay was produced on floodplains (Retallack 1990; Algeo and Scheckler 1998). Increased depth and areal extent of rooting changed soil chemistry. Carbon sequestration (by increased soil silicate formation and primary production, more recalcitrant plant biomolecules (e.g. lignin), and burial of trunks, roots, and branches in marine and terrestrial sediments) transformed global atmospheric chemistry (less CO_2, more O_2). Global cooling, pronounced extinctions of marine invertebrates, and the initiation of wildfire conflagrations are among the effects that can be attributed to afforestation (Beerbower *et al.* 1992; Berner 1997, 1998; Algeo and Scheckler 1998).

References

Algeo, T.J. and Scheckler, S.E. (1998) Terrestrial–marine teleconnections in the Devonian: links between the evolution of land plants, weathering processes, and marine anoxic events. *Philosophical Transactions of the Royal Society of London B* **353**, 113–130.

Beck, C.B., ed. (1988) *Origin and evolution of gymnosperms*. Columbia University Press, New York.

Beerbower, R., Boy, J.A., DiMichele, W.A., Gastaldo, R.A., Hook, R., Hotton, N., Phillips, T.L., Scheckler, S.E. and Shear, W.A. (1992) Paleozoic terrestrial ecosystems (compiled by W.A. DiMichele and R. Hook). In: A.K. Behrensmeyer, J.D. Damuth, W.A. DiMichele, R. Potts, H.-D. Sues and S.L. Wing, eds. *Terrestrial ecosystems through time*, pp. 204–325. University of Chicago Press, Chicago.

Berner, R.A. (1997) The rise of plants and their effect on weathering and atmospheric CO_2. *Science* **276**, 544–546.

Berner, R.A. (1998) The carbon cycle and CO_2 over Phanerozoic time: the role of land plants. *Philosophical Transactions of the Royal Society of London B* **353**, 75–82.

Chaloner, W.G. and Sheerin, A. (1979) Devonian macrofloras. In: M.R. House, C.T. Scrutton and M.G. Bassett, eds. *The Devonian System*, pp. 145–161. Special Papers in Palaeontology no. 23.

Retallack, G.J. (1990) *Soils of the past: an introduction to paleopedology*. Harper Collins Academic, London.

Stewart, W.N. and Rothwell, G.W. (1993) *Paleobotany and the evolution of plants*. Cambridge University Press, Cambridge.

Taylor, T.N. and Taylor, E.L. (1993) *The biology and evolution of fossil plants*. Prentice Hall, Englewood Cliffs, New Jersey.

1.3.6 Terrestrialization of Animals

P.A. SELDEN

Introduction

The diversity of animals on land greatly exceeds that in the sea; this is almost entirely accounted for by the insects, which make up 70% of all animal species alive today. However, of over 30 animal phyla, only the arthropods, molluscs, annelids, and vertebrates have significant numbers of macroscopic terrestrial representatives. A larger set of phyla includes those with very few terrestrial species, cryptobiotic representatives, and internal parasites on terrestrial organisms. The body plans of some highly successful marine groups seem to have precluded their terrestrialization; these include the sipunculid, echiuroid, and priapulid worms, cnidarians, lophophorates, chaetognaths, pogonophores, hemichordates, and echinoderms. No phylum originated on land, and no major terrestrial clade has become extinct, as far as is known. Outstanding questions on terrestrialization are: (1) what physiological mechanisms enabled animals to emerge on to land, and did each taxonomic group use similar mechanisms; (2) what routes on to land did animals use and did they terrestrialize simultaneously, suddenly, or gradually; and (3) how were the earliest terrestrial ecosystems organized? Some evidence comes from comparative physiology, but palaeontology can test hypotheses based on neontology, give evidence for plant–animal interactions, and uniquely can provide the dimension of time.

Animals moving on to land from the sea experience profound changes in all aspects of life (Little 1983). On land, water supply is variable, and commonly seasonal. Oxygen is more available in air than in water because the diffusion coefficient (partial pressure per unit length) of oxygen in air is 11.0, but in water is 0.000 034, so supply of oxygen to tissues by diffusion is an option in terrestrial animals with small cross-sections. Support is more of a concern in the less viscous aerial medium than in water, but once this problem is overcome, locomotion becomes easier and faster. The difference in refractive index between air and water poses a problem for visual sense organs in transition, but high-frequency vibrations can be perceived more easily in air, resulting in a greater use of sound by terrestrial animals. On land, internal fertilization is the norm, and greater protection (e.g. from drought) is necessary for the developing embryos. Changes in nutrition, ion balance regulation, and excretion are also necessary for terrestrialization.

Four groups of land animals can be defined on their management of water availability. (1) Aquatic animals avoid the problem by living in interstitial water in soils; these include microscopic protozoans, ostracods, and nematodes. (2) Cryptic forms differ from those in group 1 by being macroscopic, but similarly inhabit environments of constantly high humidity, such as soil and tropical forest litter; included in this group are earthworms, leeches, flatworms, isopods, slugs, insect larvae, and some amphibians and myriapods. (3) Poikilohydric (desiccation-tolerant) organisms require high humidity to function but can tolerate desiccation by rehydrating when conditions become favourable again; cryptobiotic rotifers and mites belong to this group, as do some animals with desiccation-tolerant dormant stages, such as the eggs of fairy shrimps and tardigrade tuns (cysts). (4) Homoiohydric organisms have achieved the true conquest of the land by the use of waterproof cuticles, transport systems, and osmoregulation; in this group are tetrapods, insects, arachnids, and some isopods and molluscs.

Many terrestrial animals took the littoral route on to land; living in the highly variable environment of the seashore gave them preadaptations for life on land. Others took different routes, via fresh water for example, and there is evidence that some Late Silurian terrestrial biotas occupied a saltmarsh habitat.

Fossil evidence of terrestrialization

There are two main types of fossil evidence for terrestrial life: body fossils and trace fossils—direct and indirect evidence, respectively. Trace fossils include burrows and trackways in subaerial sediments, coprolites, and plant damage; other evidence for terrestrial life, such as chemical fossils, could be included here. Trace fossils can provide evidence that animals were present on land, possibly what they were doing, but not necessarily what kind of animal left the traces. Body fossils give direct indications of the type of animal present, but it may be unclear whether or not it lived in a terrestrial environment. Commonly, the nature of the sediment provides the clue to terrestriality. However, there are some good morphological indicators: gills and lungs have different

morphologies, with the latter normally being enclosed in the body and connected to the outside by stigmata; trichobothria are fine hairs sensitive to airborne vibrations which could not function in water; a hanging stance, plantigrade foot, and leg-rocking joints occur in land arthropods; and copulatory systems are generally necessary in terrestrial animals but not aquatic ones.

Body fossils

A study of the fossil record (Fig. 1.3.6.1) reveals that modern land animal groups did not terrestrialize simultaneously. There is no fossil record of free-living terrestrial flatworms, nemerteans, or nematodes, although fossil examples of parasitic and aquatic nematodes are known, mostly from ambers. Oligochaete annelids are known from the Carboniferous, though they may not have been terrestrial at that time. Two groups of land snails, helicinid prosobranchs and stylommatophoran pulmonates, are recorded from the Upper Carboniferous. The earliest basommatophoran pulmonate is Late Jurassic in age, although basommatophorans are thought, on comparative morphological grounds, to be ancestral to other pulmonates. The development of ground shade and deciduous leaf litter (probably in the Early Carboniferous) may have been necessary before land snails could be assured of the damp conditions required for colonization. The record of Onychophora begins with marine lobopodians from the Cambrian, but no fossil terrestrial forms are known. A possible marine tardigrade larva has been described from Cambrian Orsten of Siberia. Tardigrades withstand periods of desiccation by forming cysts known as tuns. Aerial dispersal of tuns may have enabled these tiny creatures to have inhabited moist environments alongside the earliest terrestrial plants.

'Myriapods', once thought to be a monophyletic clade allied to insects, have been shown to be paraphyletic. There is insufficient evidence to confirm that supposed myriapods in Cambrian marine sediments are, in fact, arthropods, but good milliped and centiped fossils occur in Late Silurian and Devonian strata, including scutigeromorph centipeds among the earliest land animals (Jeram *et al.* 1990). By Devonian times, myriapods had reached greater ordinal diversity than today, and some reached giant proportions (2 m) in the Carboniferous forests. All extant hexapods are terrestrial or secondarily aquatic. Evidence for a closer hexapod–crustacean than hexapod–myriapod relationship is emerging, though precisely at what point(s) in the phylogeny of hexapod ancestors terrestrialization occurred is unclear. There seems to have been independent evolution of respiratory organs numerous times amongst tracheates, possibly corresponding to separate terrestrialization events. The earliest apterygotes are found in Devonian rocks, but the first pterygotes are Carboniferous in age.

Amongst chelicerates, eurypterids ranged from Ordovician to Permian and were predominantly aquatic animals, but from the Silurian onwards some were amphibious, as evidenced by their accessory lungs and subaerial trackways. They illustrate a failed attempt at terrestrialization. Scorpions, close relatives of eurypterids, succeeded in terrestrialization by converting gills into lungs. Whilst all Silurian scorpions appear to have been aquatic, book lungs appear first in Lower Devonian scorpions, and aquatic, terrestrial, and amphibious forms probably coexisted through the Devonian. All other arachnids are primarily terrestrial today. The oldest are the trigonotarbids, extinct relatives of spiders, with unequivocal terrestrial features such as book lungs. Trigonotarbids are among the oldest land animals, from the Silurian of Shropshire (Jeram *et al.* 1990), and are common in all early terrestrial ecosystems. Mites, pseudoscorpions, and spiders are also found in Devonian strata, and by Carboniferous times there were more arachnid orders than today; the spiders radiated more dramatically in later periods.

The fossil records of many crustacean groups are generally good because of their mineralized exoskeletons. However, the terrestrial groups show very short fossil ranges. The first amphipods are Upper Eocene, although it has been suggested, on biogeographical grounds, that their origins lie in the mid-to-late Mesozoic, or earlier. The terrestrial talitrids, with no fossil record, are considered by some to have emerged on to land when the first angiosperm forests became established in coastal regions. The isopods have a long fossil record, from the Upper Carboniferous, with their supposed origins in the Devonian, but the terrestrial Oniscidea are known only from the Eocene onwards. Similarly, whilst crabs and crayfish first appeared in the Jurassic, the important crab radiations did not occur until the Cretaceous and Palaeogene, with true terrestrial forms appearing in Neogene times.

No fewer than 10 genera of tetrapods are known from Late Devonian deltaic and lacustrine palaeoenvironments worldwide. Morphological and sedimentological evidence suggests that these animals were aquatic carnivores at that time. A 20 myr gap in the tetrapod record during the Early Carboniferous makes it difficult to relate these early examples to later, terrestrial forms. Tetrapod origins and evolution are discussed in Section 1.3.7.

Trace fossils

Although the first body fossils of terrestrial animals appear in the Late Silurian (Jeram *et al.* 1990), trace fossils attributed to their activities are known from the Ordovician. Trackways in subaerial deposits in the Caradocian Borrowdale Volcanic Group of north-west England may have been produced by animals making limited

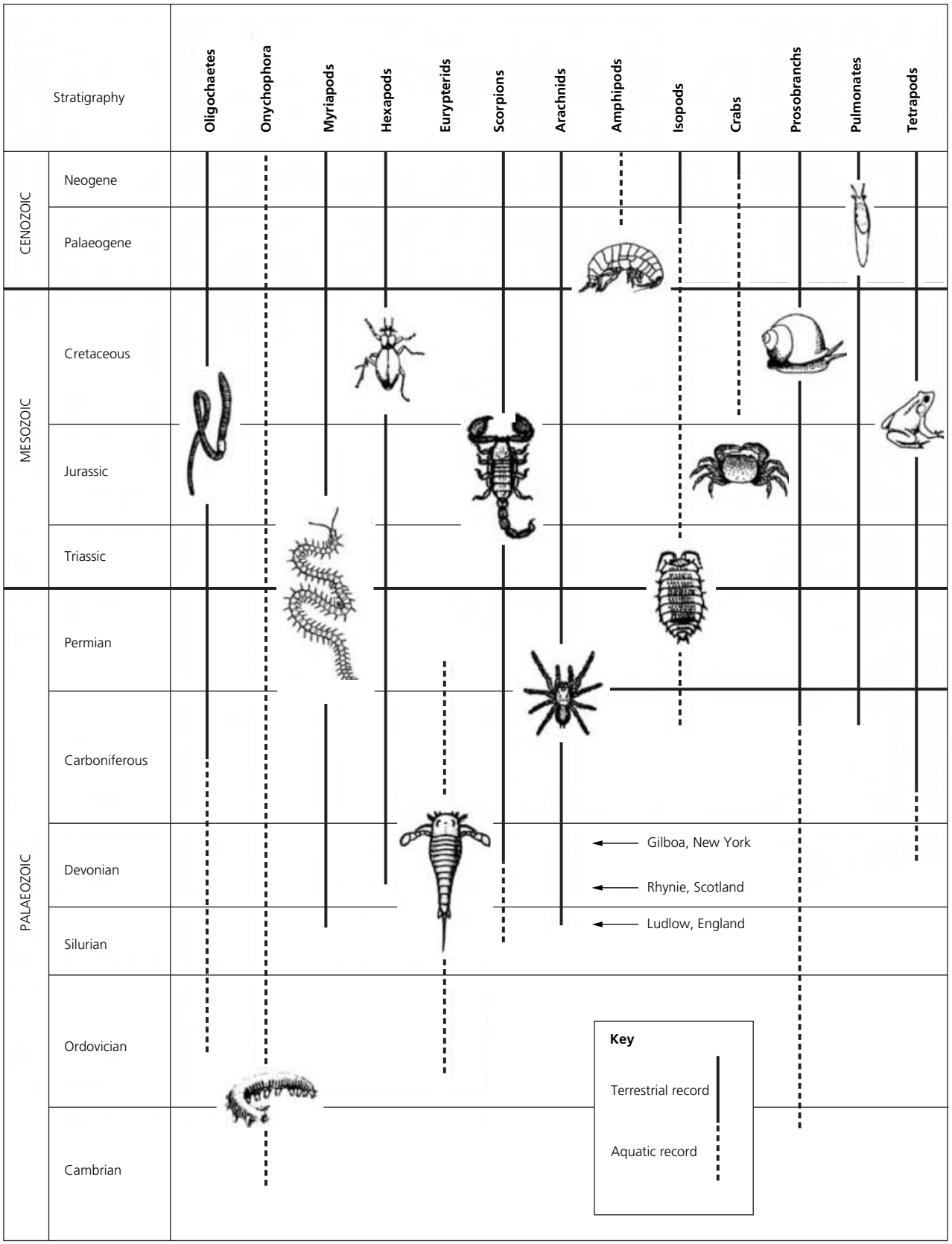


Fig. 1.3.6.1 Fossil record of terrestrial animals and their forebears, and stratigraphic positions of three major early terrestrial Lagerstätten.

excursions on to land or, indeed, they could have been terrestrial. Meandering, subvertical, back-filled burrows in an upper Ordovician palaeosol in Pennsylvania bear some resemblance to modern milliped burrows, but it is impossible to say what produced them. Late Silurian trackways, attributable to terrestrial or semiterrestrial arthropods, are relatively abundant. For example, a rich diversity of trackways and burrows in the Upper Silurian Tumblagooda Sandstone of Western Australia is considered the work of myriapods, eurypterids, scorpions, and euthycarcinoids. Whilst some were made under water, a large number represent animals walking on sediments exposed to the air, and possibly on dry, windblown sand. Annelid traces, including burrows and faecal pellets, occur in palaeosols from the Carboniferous onwards; they may have emerged on to land with the first humic soil. Evidence for terrestrial locomotion by Devonian tetrapods is ambiguous.

Another line of trace fossil evidence comes from coprolites. Coprolites bearing plant remains provide direct evidence of plant–animal interaction in early terrestrial ecosystems. Upper Silurian and Lower Devonian coprolites attributable to small arthropods have been described. For example, coprolites packed with different spore types are known from Silurian and Devonian sites in the Welsh Borderland (Edwards *et al*. 1995). The coprolites were initially thought to be sporangia, but their regular shape, lack of a sporangial wall, presence of up to nine spore types in some specimens, and other debris, ruled out this possibility. The coprolites were probably produced by terrestrial detritivores (litter-feeders) which were ingesting spores and spore masses but not digesting them, in a similar way to modern millipeds. Plant damage, probably caused by arthropods, is common in some early terrestrial ecosystems, such as the Rhynie chert (see Section 3.4.5). Damaged specimens of *Psilophyton* from the Lower Devonian of Gaspé, Québec, include several types of wounding and wound reaction, suggesting attack by animals with sucking mouthparts and subsequent response by the plants. Possible coprolites were also found both within and outside these plant stems. It is likely that the main interactions between plants and animals in the earliest terrestrial ecosystems were directly through sap-feeders and indirectly through litter decomposers.

Ecosystems

The best-known early terrestrial Lagerstätte is still the Rhynie chert (396 Ma) of Scotland, first described in detail in the 1920s (see Section 3.4.5). Over the last 30 years, however, a number of other early terrestrial ecosystems have become almost as well studied (Fig. 1.3.6.1), including the Gilboa, New York, and Ludlow, England, Lagerstätten (see reviews: Shear 1991; Edwards and Selden 1993; Shear and Selden, in press). This work has revealed that the familiar plant–herbivore–carnivore food chain of today's world had not evolved by the Devonian period. The animals present in Siluro-Devonian Lagerstätten were either carnivores (e.g. arachnids, centipeds) or occupied the decomposer niche (e.g. Collembola, millipeds). Tetrapod herbivory is not known before the Late Carboniferous. In fact, many modern food chains, such as the soil ecosystem, are decomposer-based, and herbivores commonly rely on gut microorganisms to break down green plant matter before it can be ingested. The evolution of herbivory may have been a result of gradual short-circuiting of the decomposer food chain by animals harbouring decomposing microorganisms in their guts, thus enabling the aerial parts of green plants to be eaten. The development of the tree habit may have provided a stimulus in this direction.

References

Edwards, D. and Selden, P.A. (1993) The development of early terrestrial ecosystems. *Botanical Journal of Scotland* **46**, 337–366.

Edwards, D., Selden, P.A., Richardson, J.B. and Axe, L. (1995) Coprolites as evidence for plant–animal interaction in Siluro-Devonian terrestrial ecosystems. *Nature* **377**, 329–331.

Jeram, A.J., Selden, P.A. and Edwards, D. (1990) Land animals in the Silurian: arachnids and myriapods from Shropshire, England. *Science* **250**, 658–666.

Little, C. (1983) *The colonisation of land*. Cambridge University Press, Cambridge.

Shear, W.A. (1991) The early development of terrestrial ecosystems. *Nature* **351**, 283–289.

Shear, W.A. and Selden, P.A. (in press) Rustling in the undergrowth: animals in early terrestrial ecosystems. In: P.G. Gensel and D. Edwards, eds. *Plants invade the land: evolutionary and environmental perspectives*. Columbia University Press, New York.

1.3.7 Origin of Tetrapods

M.I. COATES

Introduction

The origin of tetrapods, i.e. amniotes (mammals, birds, reptiles) and amphibians (frogs/toads, salamanders, apodans), has been linked traditionally to vertebrate terrestrialization. Scenarios of this key event usually include sparsely vegetated, seasonally arid Devonian

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excursions on to land or, indeed, they could have been terrestrial. Meandering, subvertical, back-filled burrows in an upper Ordovician palaeosol in Pennsylvania bear some resemblance to modern milliped burrows, but it is impossible to say what produced them. Late Silurian trackways, attributable to terrestrial or semiterrestrial arthropods, are relatively abundant. For example, a rich diversity of trackways and burrows in the Upper Silurian Tumblagooda Sandstone of Western Australia is considered the work of myriapods, eurypterids, scorpions, and euthycarcinoids. Whilst some were made under water, a large number represent animals walking on sediments exposed to the air, and possibly on dry, windblown sand. Annelid traces, including burrows and faecal pellets, occur in palaeosols from the Carboniferous onwards; they may have emerged on to land with the first humic soil. Evidence for terrestrial locomotion by Devonian tetrapods is ambiguous.

Another line of trace fossil evidence comes from coprolites. Coprolites bearing plant remains provide direct evidence of plant–animal interaction in early terrestrial ecosystems. Upper Silurian and Lower Devonian coprolites attributable to small arthropods have been described. For example, coprolites packed with different spore types are known from Silurian and Devonian sites in the Welsh Borderland (Edwards *et al*. 1995). The coprolites were initially thought to be sporangia, but their regular shape, lack of a sporangial wall, presence of up to nine spore types in some specimens, and other debris, ruled out this possibility. The coprolites were probably produced by terrestrial detritivores (litter-feeders) which were ingesting spores and spore masses but not digesting them, in a similar way to modern millipeds. Plant damage, probably caused by arthropods, is common in some early terrestrial ecosystems, such as the Rhynie chert (see Section 3.4.5). Damaged specimens of *Psilophyton* from the Lower Devonian of Gaspé, Québec, include several types of wounding and wound reaction, suggesting attack by animals with sucking mouthparts and subsequent response by the plants. Possible coprolites were also found both within and outside these plant stems. It is likely that the main interactions between plants and animals in the earliest terrestrial ecosystems were directly through sap-feeders and indirectly through litter decomposers.

Ecosystems

The best-known early terrestrial Lagerstätte is still the Rhynie chert (396 Ma) of Scotland, first described in detail in the 1920s (see Section 3.4.5). Over the last 30 years, however, a number of other early terrestrial ecosystems have become almost as well studied (Fig. 1.3.6.1), including the Gilboa, New York, and Ludlow, England, Lagerstätten (see reviews: Shear 1991; Edwards and Selden 1993; Shear and Selden, in press). This work has revealed that the familiar plant–herbivore–carnivore food chain of today's world had not evolved by the Devonian period. The animals present in Siluro-Devonian Lagerstätten were either carnivores (e.g. arachnids, centipeds) or occupied the decomposer niche (e.g. Collembola, millipeds). Tetrapod herbivory is not known before the Late Carboniferous. In fact, many modern food chains, such as the soil ecosystem, are decomposer-based, and herbivores commonly rely on gut microorganisms to break down green plant matter before it can be ingested. The evolution of herbivory may have been a result of gradual short-circuiting of the decomposer food chain by animals harbouring decomposing microorganisms in their guts, thus enabling the aerial parts of green plants to be eaten. The development of the tree habit may have provided a stimulus in this direction.

References

Edwards, D. and Selden, P.A. (1993) The development of early terrestrial ecosystems. *Botanical Journal of Scotland* **46**, 337–366.

Edwards, D., Selden, P.A., Richardson, J.B. and Axe, L. (1995) Coprolites as evidence for plant–animal interaction in Siluro-Devonian terrestrial ecosystems. *Nature* **377**, 329–331.

Jeram, A.J., Selden, P.A. and Edwards, D. (1990) Land animals in the Silurian: arachnids and myriapods from Shropshire, England. *Science* **250**, 658–666.

Little, C. (1983) *The colonisation of land*. Cambridge University Press, Cambridge.

Shear, W.A. (1991) The early development of terrestrial ecosystems. *Nature* **351**, 283–289.

Shear, W.A. and Selden, P.A. (in press) Rustling in the undergrowth: animals in early terrestrial ecosystems. In: P.G. Gensel and D. Edwards, eds. *Plants invade the land: evolutionary and environmental perspectives*. Columbia University Press, New York.

1.3.7 Origin of Tetrapods

M.I. COATES

Introduction

The origin of tetrapods, i.e. amniotes (mammals, birds, reptiles) and amphibians (frogs/toads, salamanders, apodans), has been linked traditionally to vertebrate terrestrialization. Scenarios of this key event usually include sparsely vegetated, seasonally arid Devonian

floodplains or coastal mud flats, thus favouring air-breathing fishes able to struggle from one drying pool to another (see Ahlberg and Milner 1994; Clack 1997). Lobe-fins (sarcopterygians) have long been recognized as including candidates most likely to survive such conditions. Of these, *Eusthenopteron* (Fig. 1.3.7.1a), the best-known member of the extinct osteolepiforms, has often been illustrated as an actual tetrapod forebear, half emerged, on the banks of some Palaeozoic swamp or shoreline. The anticipated ancestor–descendant sequence was apparently confirmed in the 1930s and 1950s by discoveries in East Greenland of Devonian (Famennian) tetrapods: near-complete skeletal remains of *Ichthyostega* (Fig. 1.3.7.1d) and incomplete skulls of *Acanthostega* and *Ichthyostegopsis* (see Coates 1996). *Ichthyostega* fulfilled expectations by incorporating a fish-like notochordal braincase, subopercular bone, and a ray-supported tail-fin within an otherwise tetrapod-like skeleton. Such primitive features have remained conspicuously absent from published accounts of Carboniferous coal-measure, and earlier, tetrapods (Ahlberg and Milner 1994).

Prior to the late 1980s, research on tetrapod origins developed in two principal directions. First, descriptions of further Carboniferous and Permian taxa broadened knowledge about Palaeozoic tetrapod diversity and led to the recognition of (and conflicting hypotheses about) major taxonomic groups (Ahlberg and Milner 1994). These include baphetids (loxommatids), colosteids, aïstopods, nectrideans, and microsaurs, together with possible amphibian relatives (temnospondyls, e.g. *Balanerpeton*, Fig. 1.3.7.1e) and possible amniote relatives (anthracosaurs and captorhinids). These discoveries occurred within a small number of well-documented fossil ecosystems, extending knowledge of early tetrapod habitats from the Famennian floodplains and mud flats of East Greenland to sites such as the Viséan shallow lake of East Kirkton and the Westphalian deltas and coal-

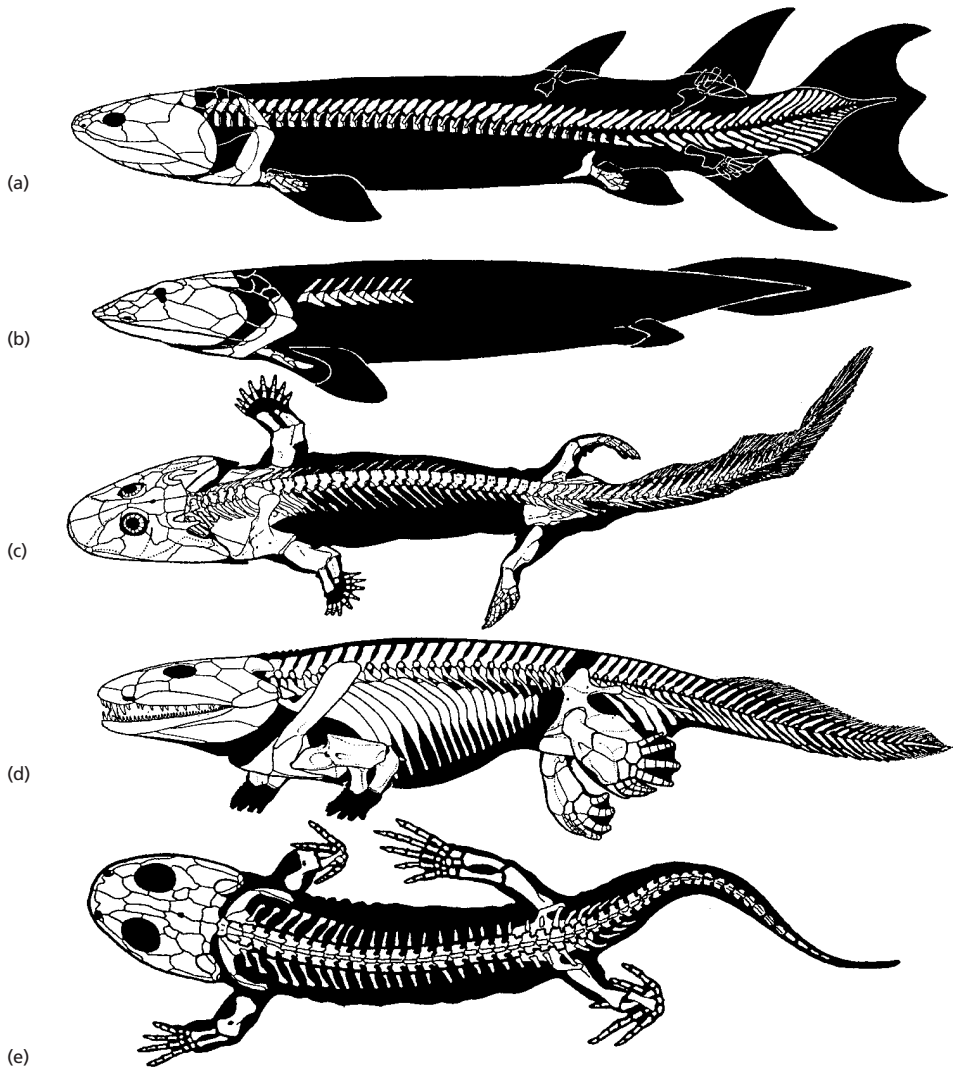


Fig. 1.3.7.1 Silhouette diagrams of tetrapod total-group members. (a) *Eusthenopteron* (Osteolepiformes; Mid–Upper Devonian). (b) *Panderichthys* (Panderichthyidae; Mid–Upper Devonian). (c) *Acanthostega* (plesion stem-tetrapod; Upper Devonian). (d) *Ichthyostega* (plesion stem-tetrapod; Upper Devonian; new reconstruction including caudal ribs). (e) *Balanerpeton* (Temnospondyli; Viséan). In (a) and (b) fin-rays and scales are omitted, while dermal bones of opercular flap, upper shoulder girdle, and rear of the skull roof, plus endoskeletal fin supports are shown in outline only; in (c) gastralia, carpal and tarsal osteoderms are omitted. This convention is intended to clarify comparison of retained skeletal features throughout the genera illustrated.

swamps of Nyrany (Czech Republic), Mazon Creek (Illinois), and Joggins (Nova Scotia) (Ahlberg and Milner 1994; Clack 1998).

Second, the application of cladistic methodology to sarcopterygian and tetrapod interrelationships provided a more rigorous framework within which to examine theories of tetrapod origin (see Ahlberg and Milner 1994). One new phylogeny challenged assumptions about the ancestral relation of osteolepiforms to tetrapods, and proposed lungfish as the tetrapod sister-group. An alternative model retained lungfish as the extant sister-group (cf. Fig. 1.3.7.2), but also presented a series of osteolepiform–tetrapod synapomorphies. These included features of the pectoral fin and girdle, as well as resolving arguments about the choana (the internal nostril shared by all tetrapods and certain sarcopterygians). Significantly, this work foreshadowed subsequent studies which identified the importance of fossils for determining primitive conditions and character polarity.

Cladistic techniques also helped to clarify the anatomical gulf between osteolepiforms and *Ichthyostega* plus more advanced Carboniferous genera, by means of specifying, on a character by character basis, the mor-

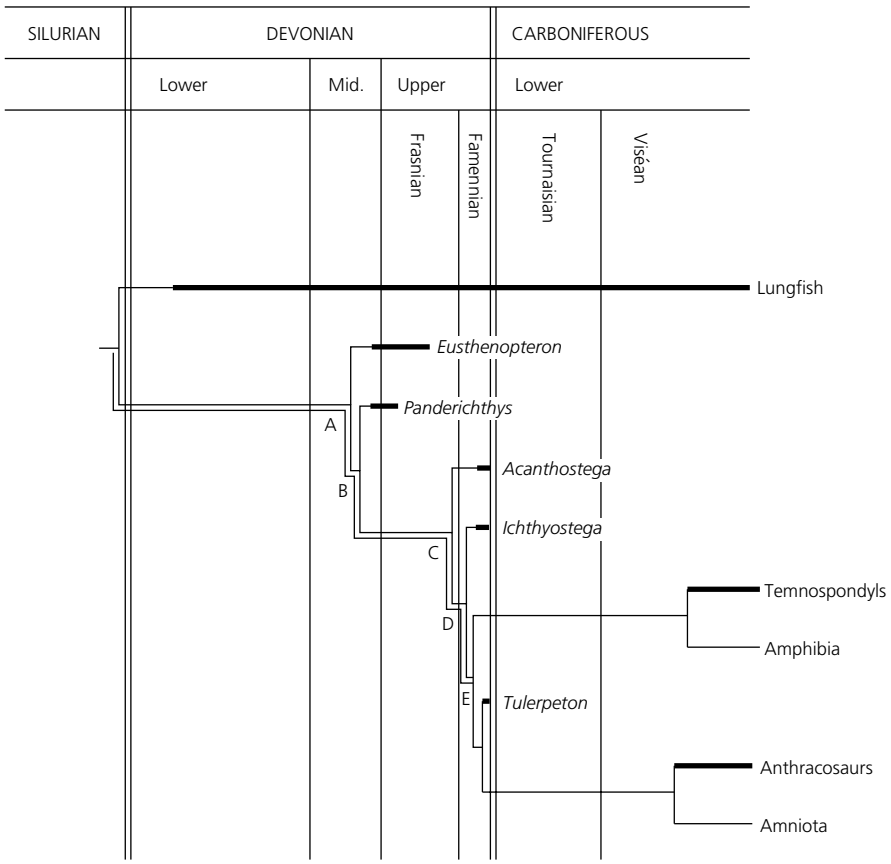


Fig. 1.3.7.2 Phylogenetic tree of the tetrapod stem-group and basal crown-group radiation, excluding less completely known taxa and many Carboniferous tetrapod clades. Node A is node uniting *Eusthenopteron* and higher tetrapods; not the base of the tetrapod stem, the defining characters of which are uncertain. Node E is base of tetrapod crown-group; extent of stem-group marked by double line. Node A: palatal nostril present; shoulder girdle with socket; humeral head convex. Node B: skull flattened dorsoventrally; snout length increased; orbits dorsal; frontal bones present; body flattened dorsoventrally; dorsal and anal fins absent; elongate leaf-shaped tail fin; ribs enlarged; shoulder girdle enlarged; humerus flattened dorsoventrally. Node C: nasal bones meet at midline; compact undivided braincase; opercular bone series absent; prepelvic vertebrae interarticulate; ribs two-headed; fish-like dermal bones reduced/lost from shoulder girdle; rudimentary scapular blade; loss of fin-rays from pectoral and pelvic appendages; digits present; simple ankle and wrist; pelvis enlarged; sacrum present. Node D: ulnar olecranon process (weight-supporting elbow joint); tail fin reduced; more tetrapod-like, robust shoulder girdle; pelvic girdle with greater buttressing. Node E: cranial sensory lines in grooves; occipital condyles present (consolidated neck joint); scapular blade well developed; complex wrist and ankle joints; tail fin-rays and internal skeletal supports absent. (Adapted primarily from Coates 1996; with taxon ranges from Clack 1997; selected characters supporting nodes A–E adapted from Ahlberg and Milner 1994 and Coates 1996.)

phological differences and similarities between fish-like and tetrapod-like anatomies. However, the fish–tetrapod transition can now be addressed in much greater detail following the discovery of new data on panderichthyids (Fig. 1.3.7.1b), a sarcopterygian group yielding increasingly tetrapod-like characteristics; new specimens of *Acanthostega* and *Ichthyostega*; the discovery of a Russian Famennian tetrapod, *Tulerpeton*; and the identification of Late Devonian tetrapod fragments from Pennsylvania, Scotland, Latvia, and Australia.

New data: *Panderichthys*, *Acanthostega*, *Ichthyostega*, and others

Panderichthyids include *Panderichthys* (Fig. 1.3.7.1b) and *Elpistostege* (Clack 1997) from the Frasnian of Latvia and Canada, respectively. They possess tetrapod-like dorsally placed orbits, flattened skulls, enlarged ribs, fin distribution, and details of humeral morphology (Coates 1996). However, these apparently advanced characters are associated with primitive features such as a jointed braincase resembling the generalized sarcopterygian condition (Carroll 1996), and many key skeletal features (such as the pelvic girdle and fin supports) remain undescribed. Given their likely phylogenetic proximity to tetrapods it is probably significant that, unlike the pike-shaped *Eusthenopteron* (Fig. 1.3.7.1a), the tetrapod-like body form of panderichthyids indicates a shallow-water predatory niche (Ahlberg and Milner 1994).

Specimens of *Acanthostega* (Fig. 1.3.7.1c) collected in 1987 reveal the most completely known skeletal anatomy of any Devonian tetrapod (Coates 1996 and references therein). Superficially, *Acanthostega* resembles a generalized Carboniferous tetrapod, but numerous aspects are even more fish-like than those of *Ichthyostega*. These include a larger ray-supported tail fin; an axial skeleton with a barely regionalized neck; short ribs in which the two heads (characteristic of tetrapod ribs) are only weakly differentiated; a shoulder girdle retaining a flange (postbranchial lamina) usually associated with the rear of an internal gill chamber; sensory canals fully enclosed within skull bones; and a branchial skeleton including a massive ceratohyal plus at least three gill arches. Its eight-digit limbs include a radius and ulna resembling those of *Panderichthys* and *Eusthenopteron*, while the broad, flat tibia and fibula articulate with a simple ankle like that of *Ichthyostega* (Fig. 1.3.7.1d).

Polydactyly has emerged as an unanticipated feature of all known Devonian tetrapods (Coates 1996). *Acanthostega* limb patterns are matched by the six-digit limbs of *Tulerpeton* and what has turned out to be the seven-digit hindlimb of *Ichthyostega* (Coates 1996). Absence of complex wrists and ankles in *Acanthostega* and *Ichthyostega* is probably primitive relative to conditions in *Tulerpeton* and more advanced tetrapods. This is consistent with the more conventionally tetrapod-like tibia and fibula of *Tulerpeton* and the presence of ankle characteristics shared with Carboniferous tetrapods and especially anthracosaurs (Coates 1996).

Although several details of the anatomy of *Ichthyostega* are unknown (the neck, sacrum, wrist, and forelimb digits; Fig. 1.3.7.1d), it is increasingly clear that it differs considerably from *Acanthostega* and any other Palaeozoic tetrapod known in significant detail (Coates 1996). The large forelimb, flexed permanently at the elbow, combined with a hindlimb resembling a cetacean flipper, indicates a resting body-posture like that of a seal rather than more conventional primitive tetrapod analogues. Furthermore, the caudal ribs, just behind the pelvis, are unusually massive and bladed like the series enclosing the trunk (Fig. 1.3.7.1d), but the functional significance of these is obscure (beyond insertion for musculature).

Abundant detailed information about the East Greenland tetrapods has accelerated the identification and corroboration of fragmentary remains attributed to Devonian tetrapods, and at least five further genera have been recognized from sites in Australia, Latvia, Scotland, and North America (Carroll 1996; Coates 1996). Increased Devonian tetrapod skeletal data have likewise informed interpretations of possible trackway evidence. A recent survey identifies the most plausible examples as those known from the Devonian of Australia, Scotland, and Ireland (Clack 1997).

Like the Devonian tetrapod catalogue, the Carboniferous record has also been enriched by new taxa and localities. Nevertheless, a real problem persists with the dearth of specimens from the Tournaisian and lower Viséan (Fig. 1.3.7.2). The crucial contents of this gap of at least 25 million years are predicted by the range of tetrapods found in sites such as East Kirkton, from the Scottish Viséan (Clack 1998). East Kirkton is one of the earliest definitively terrestrial tetrapod localities. In addition to numerous plants, invertebrates, and somewhat fragmentary fish remains, this fauna also includes likely stem-amniotes, stem-amphibians, and representatives of groups whose affinities are much less well understood (Clack 1998). Such sudden diversity, relative to the Devonian record, emphasizes the point that numerous, fundamental, branching events in tetrapod phylogeny must have occurred in the Early Carboniferous. Other notable additions to the list of Carboniferous sites include the Viséan St Louis Formation of Delta, Iowa, including a primitive anthracosaur-like species (Coates 1996), and the discovery of a similarly aged tetrapod locality in Australia (Milner 1996).

New patterns and possible processes across the fish–tetrapod divide

These new data have contributed to several reanalyses of primitive tetrapod phylogeny. Representative cladograms such as those in Ahlberg and Milner (1994), Carroll (1996), Coates (1996; summarized in Fig. 1.3.7.2), and Clack (1998) share important features. Perhaps most significantly, *Panderichthys*, *Acanthostega*, and *Ichthyostega* emerge consistently as successive sister-groups to the basal radiation of the lineages leading to modern amphibians and amniotes (cf. Fig. 1.3.7.2). It seems likely that this sequence will be a robust feature of future phylogenies. Major differences between such trees increasingly concern the position of the node from which modern tetrapod diversity radiates. At one extreme, attachment of *Tulerpeton* to the amniote basal lineage implies that amphibian and amniote evolutionary histories diverged before the end of the Devonian (Fig. 1.3.7.2). At the other extreme, the amphibian–amniote divergence is placed much higher in the tree; temnospondyls are divorced from amphibians, and anthracosaurs are divorced from amniotes (cf. relationships discussed in Ahlberg and Milner 1994; Coates 1996). However, despite such major differences in tree topology, it is noteworthy that both versions of tetrapod evolution imply that amphibian and amniote ancestries diverged before the mid-Viséan.

With the possible exception of the temnospondyl *Balanerpeton* (Fig. 1.3.7.1e), all taxa shown in Fig. 1.3.7.1 can therefore be described as 'stem-tetrapods' and used to illustrate anatomical transformations spanning the traditionally accepted locus of the fish–tetrapod divide. Paradoxically, the origins of the tetrapod total-group (*all* taxa that are related more closely to the modern tetrapods than they are to lungfishes) and crown-group (the latest common ancestor of living tetrapods and all of its descendants) are thus distanced from the origin of limbs, important features of which (digits, carpus, and tarsus) appear between nodes B and C (Fig. 1.3.7.2) and continue to accrue, piecemeal fashion, throughout the crown-group. These and other transformation patterns are already contributing to debates addressing phylogenetic questions in other aspects of vertebrate evolution. Analyses of the fin–limb transition are central to many studies of the evolution of vertebrate limb development (Coates 1996; Johanson and Ahlberg 1998), while primitive stapedial and fenestra ovalis morphologies inform questions on middle ear evolutionary neurobiology (Clack 1998).

Palaeoecological settings for the earliest tetrapods remain poorly understood. Late Devonian terrestrial environments supported architecturally modern forests (Clack 1997) and probably supplied sufficiently shady, moist, and food-rich surroundings to sustain early forays of *Ichthyostega*-like species. The global distribution of Late Devonian tetrapods is known to have extended in an equatorial belt from Euramerica to East Gondwana. However, this pattern changes dramatically after the Lower Carboniferous, with the apparent loss of tetrapods from East Gondwana as it drifted southwards into the zone of the late Palaeozoic glaciation (Milner 1996). Compared with the classic scenarios of *Eusthenopteron* lurching between ephemeral pools, Devonian tetrapod habitats now appear more aquatic. Sedimentological data show that *Acanthostega* specimens are restricted to vegetation-choked active channels in a meandering river system, *Ichthyostega* originates from closely related deposits, and *Tulerpeton* comes from sediments indicative of a shallow, warm, epicontinental sea (Clack 1997). Anatomical data show that *Acanthostega* was fundamentally non-terrestrial, a gill-breather with paddle-like limbs and a large tail fin, while the extraordinary limb combination of *Ichthyostega* suggests that, at most, it was suited to only limited terrestrial excursions. These stem-tetrapods therefore appear to have continued the shallow-water habits of their *Panderichthys*-like forebears. Consequently, most features considered characteristic of tetrapods probably evolved *before* terrestrialization (see character-state changes listed from nodes B to D in Fig. 1.3.7.2).

Finally, one of the more intriguing questions arising from this revised picture of the fish–tetrapod transition concerns the rate and magnitude of evolutionary change. Combined morphological, ichnological, and phylogenetic evidence suggests that neither digited limbs nor crown-group tetrapods originated before the Frasnian (Clack 1997). The branching pattern in Fig. 1.3.7.2 may therefore illustrate a concentrated series of evolutionary events compressed into the Upper Devonian. Discussion about whether this reflects special developmental processes and/or qualifies as an episode of Simpsonian 'quantum evolution' (the idea that evolution occurs more rapidly at the origin of large-scale groups) has already begun (Carroll 1996). However, it seems equally likely that this reflects relative ignorance of neighbouring areas on the tree: the gap in the fossil record of critical forms during the Tournaisian, and the need for more information about the evolutionary diversification of primitive osteolepiform-like fishes (cf. Johanson and Ahlberg 1998).

References

Ahlberg, P.E. and Milner, A.R. (1994) The origin and early diversification of tetrapods. *Nature* **368**, 507–514.

Carroll, R.L. (1996) Revealing the patterns of macroevolution. *Nature* **381**, 19–20.

Clack, J.A. (1997) Devonian tetrapod trackways and trackmakers: a review of the fossils and footprints. *Palaeogeography, Palaeoclimatology, Palaeoecology* **130**, 227–250.

Clack, J.A. (1998) A new Early Carboniferous tetrapod with a *mélange* of crown-group characters. *Nature* **394**, 66–69.

Coates, M.I. (1996) The Devonian tetrapod *Acanthostega gunnari* Jarvik: postcranial anatomy, basal tetrapod interrelationships and patterns of skeletal evolution. *Transactions of the Royal Society of Edinburgh, Earth Sciences* **87**, 362–421.
Johanson, Z. and Ahlberg, P.E. (1998) A complete primitive rhizodont from Australia. *Nature* **394**, 569–573.
Milner, A.R. (1996) Early amphibian globetrotters? *Nature* **381**, 741–742.

1.3.8 Carboniferous Coal-swamp Forests

W.A. DIMICHELE

Introduction

The 'coal swamp' is one of the most powerful images in palaeontology. Dense, dark, and damp—populated by strange trees, giant dragonflies, and sluggish tetrapods resting on rotting logs—a diorama can be found in almost every museum and is short-hand for the Carboniferous tropics. However appealing, this visual representation of the coal-swamp forest, based on analogy with modern tropical rainforests, is largely inaccurate. Carboniferous tropical plants were drawn from at least four classes and more than 10 orders, differing widely from each other in body plan and reproductive biology. The modern tropics, by comparison, are dominated mainly by flowering plants, an admittedly diverse yet phylogenetically restricted group. Coal-swamp plants have no modern analogues, thus requiring care when using today's forests as dynamic models for the ancient past.

What is a 'coal swamp'?

In broadest terms, coal swamps are mires—wet environments in which organic matter accumulates. Mires can be classified broadly along a physical gradient that simultaneously describes their three-dimensional geometry, nutrient, and hydrological status. In planar mires the surface is below or at water table for much of the year and ground water includes mineral nutrients; hence these mires are termed minerotrophic or rheotrophic. The Florida Everglades are a modern example. In domed, or ombrotrophic, mires peat forms above the regional water table with water input mainly from rainfall, creating nutrient starvation in more interior areas. Modern Sumatra is covered by ombrotrophic mires. Both types of mire likely existed during the Carboniferous, in proportions reflecting both local conditions and regional to global climate dynamics (Cecil 1990).

The coal-swamp environment was ecologically complex and included physical phenomena similar to those found in modern wetlands. Charcoal, for example, is a common component of Carboniferous coals. Charcoal layers several centimetres thick and hundreds of metres in lateral extent occur in coal beds and record conflagrations similar to those described in modern mires during droughts. Conversely, flooding brought many coal swamps to an end; tree stumps and logs are common in roof shales, raising the image of dead snags bordering the margins of man-made lakes. Tree falls and blowdowns also have been recorded from the coal–roof shale interface and from the patterns of macrofossil plant distribution within coal beds themselves (Wnuk and Pfefferkorn 1987).

The Late Carboniferous and Early Permian were global icehouse times (Gastaldo *et al.* 1996). Coal swamps reformed intermittently in the tropical lowlands in response to global climate and sea-level fluctuations. Mires are strong indicators of high rainfall, and perhaps relatively cooler temperatures in the tropics. The intercalation of coals and palaeosols indicative of seasonal moisture stress, and the cyclic alternation of marine and terrestrial sequences, indicate that the Carboniferous tropics were not climatically uniform through time.

Coals derived from tropical mires occur mainly in the upper parts of the Lower Carboniferous and throughout the Upper Carboniferous in Europe and North America. Euramerican climates became increasingly seasonally dry during the Early Permian and the locus of peat formation moved to the Chinese microcontinents, where typically Carboniferous coal-swamp floras survived into the Late Permian (Ziegler 1990).

The major plant groups

Coal swamps were forested ecosystems composed of five major tree groups. The growth architectures (Fig. 1.3.8.1), biologies, and ecologies of these groups were distinctively different and contributed to plant assemblages that were strongly differentiated by habitat (DiMichele and Phillips 1994).

The dominant plants of the wettest parts of Westphalian coal swamps were tree lycopsids, colloquially known as giant club mosses. Lycopsid trees reached 30 m in height and over 1 m in diameter at the base. They were supported by thick bark and had a small water conducting cylinder, separating the support and water conduction functions. Growth was determinate; many species produced crowns only in the final phases of life, coincident with cone production (a monocarpic reproductive strategy). Thus the analogy to modern dicot trees seen in reconstructions is incorrect. Lycopsid trees likely formed very open forests, spending most of their life cycle as unbranched poles. Height growth and crown formation

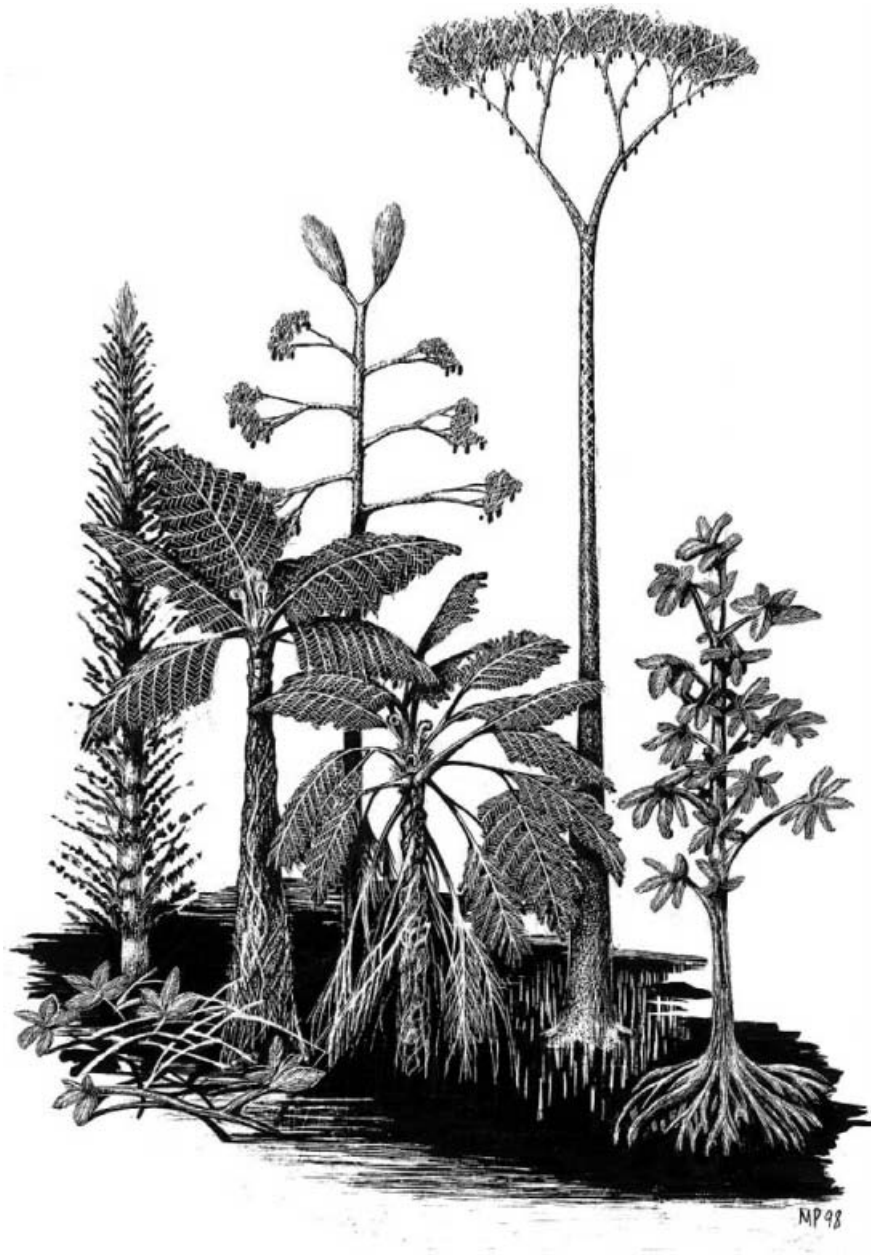


Fig. 1.3.8.1 Reconstructed growth habits of reproductively mature, selected Late Carboniferous coal-swamp plants. From left to right: a calamite tree; a scrambling cordaite; the tree fern *Psaronius*; the polycarpic lycopsid tree *Diaphorodendron scleroticum*; the seed fern *Medullosa*; the monocarpic lycopsid tree *Synchysidendron resinosum*; a mangrove cordaite tree. Maximum height is greater than 30 m. (Drawing by Mary Parrish.)

were intimately related to reproduction and dispersal rather than light capture. One group produced female reproductive organs that closely approached seeds in general morphology. Important stem genera are *Lepidodendron*, *Lepidophloios*, and *Sigillaria* among others. Roots are known as *Stigmaria*.

Cordaites were also dominant in some middle Westphalian mires. They were small, woody, seed-plant trees, similar in construction and reproductive biology to extant conifers, although with strap-like rather than needle-shaped leaves. Some cordaites have been interpreted as mangroves, based on prop roots and an association with marine indicators in coal beds. Cordaite-dominated fossil peats are often heavily rotted and cordaite wood is frequently bored by detritivorous arthropods, suggesting growth in periodically dry environments.

Stephanian (latest Late Carboniferous) coal swamps were dominated by marattialean tree ferns, a group still extant though not related to filicalean tree ferns of the modern tropics. The trunk of a marattialean was composed of a primary stem surrounded by a mantle of adventitious roots, which provided support for the tree habit. These roots were composed largely of air spaces, creating a 'cheap' means to attain large size. The crown was formed of fronds that could exceed 5 m in length,

packed with spore-producing reproductive organs. With massive reproduction, cheap construction, wide distribution, and low abundance, primitive Westphalian marattialeans appear to have been opportunists. They achieved large size in the Stephanian following major extinctions and vegetational reorganization. The common genus for stems is *Psaronius*; foliage is usually classified as *Pecopteris*.

Medullosan pteridosperms were small seed-plant trees that were locally important in mires throughout the Late Carboniferous. The group was dominant to subdominant in mineral-substrate floodplain habitats, and a subset of species occurred in mineral-rich, fire-prone parts of mires. Medullosans may have contributed to fires; their tissues were rich in resins, and large fronds, some over 7 m in length, may have remained attached to trunks after death. Seeds of many medullosans were over 5 cm in length. Pollen grains exceeded 300 µm in diameter, leading some to propose animal-mediated pollination. Common foliage types in mires include *Neuropteris*, *Alethopteris*, and *Linopteris*. Seeds are assigned to *Pachytesta*, stems to *Medullosa* and *Sutcliffia*.

The arborescent sphenopsids, or calamites, were closely related to modern horsetails and scouring rushes of the genus *Equisetum*. They were segmented, like modern horsetails, with all organs borne in whorls on supporting axes. Unlike their modern relatives, the calamites were woody, although the wood was notably parenchymatous. Common in disturbed, aggradational environments, such as stream and lake margins, sphenopsids were a persistent minor component of mires throughout the Late Carboniferous. They were the only arborescent group with a clonal habit, made possible by underground rhizomes. The common stem genus is *Calamites*. Foliage is assigned to *Annularia* and *Asterophyllites*.

Coal-swamp history

For over nine million years Westphalian coal swamps were dominated mainly by lycopsids and cordaites. The dominance of these groups reflects the commonness of the environments for which they were ecologically specialized: wet to flooded in the case of most lycopsids and periodically dry in the case of cordaites. Medullosans and specialized lycopsids occupied fire and flood prone habitats ecotonal between peat and clastic swamps. Tree ferns were interstitial opportunists in all but the wettest sites. A variety of fern and seed-plant ground cover and vines formed significant parts of this system.

Near the Westphalian–Stephanian boundary, major climatic changes, possibly associated with global warming, led to the extirpation of nearly two-thirds of coal-swamp species in the Euramerican parts of the tropics (Phillips *et al*. 1985). Most heavily affected by this

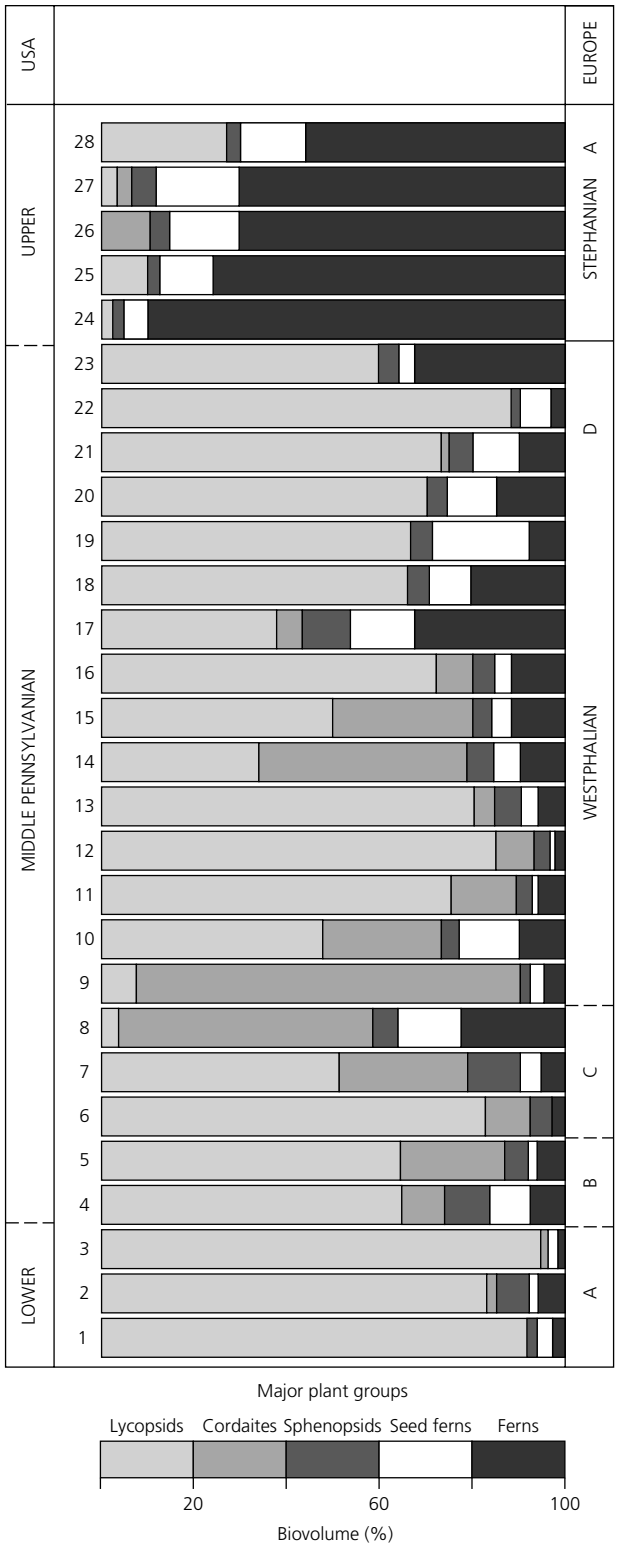


Fig. 1.3.8.2 Plant compositional changes on a seam-average basis of 28 selected Pennsylvanian (Upper Carboniferous) coals. Note major changes at the Westphalian–Stephanian boundary following extinctions of over two-thirds of the coal-swamp species. (From DiMichele and Phillips 1994; with permission from Elsevier Science.)

event were trees; over 90% of Westphalian tree species, of all taxonomic groups, failed to survive into the Stephanian. As a group, the lycopsids were devastated; all genera but *Sigillaria* disappeared from most parts of the tropics. Coal swamps with a flora very similar at the generic level to that of the Westphalian continued to survive in the Cathaysian parts of the eastern tropics into the Late Permian (Gastaldo *et al.* 1996). Climates in this part of the tropics remained aseasonally wet throughout most of the late Palaeozoic.

Stephanian mires in Euramerica were heavily dominated by marattialean tree ferns for more than six million years. Medullosan pteridosperms continued to be subdominant and, locally, the lycopsid tree *Sigillaria* was dominant in the wetter parts of mires. Furthermore, the significant floristic and vegetational differences between coal-swamp and mineral-substrate floodbasin floras that characterized the Westphalian, were much diminished during the Stephanian; tree ferns became dominant across the lowland, wetland landscape.

On either side of this major extinction and reorganization, mire vegetation was remarkably persistent, despite periodic changes in sea level and tropical climate (Fig. 1.3.8.2). Background species turnover was strongly channelled along ecomorphic lines, reflecting strong partitioning of ecological space by the major plant classes. Beginning in the Stephanian and continuing into the Permian, this ecological pattern broke down as the primitive lineages lost their position of dominance and were replaced first by ferns and then by seed plants, which remain dominant in most environments today.

References

Cecil, C.B. (1990) Paleoclimate controls on stratigraphic repetition of chemical and clastic rocks. *Geology* **18**, 533–536.

DiMichele, W.A. and Phillips, T.L. (1994) Paleobotanical and paleoecological constraints on models of peat formation in the Late Carboniferous of Euramerica. *Palaeogeography, Palaeoclimatology, Palaeoecology* **106**, 39–90.

Gastaldo, R.A., DiMichele, W.A. and Pfefferkorn, H.W. (1996) Out of the icehouse and into the greenhouse: a late Paleozoic analog for modern global vegetational change. *GSA Today* **6** (10), 1–7.

Phillips, T.L., Peppers, R.A. and DiMichele, W.A. (1985) Stratigraphic and interregional changes in Pennsylvanian coal-swamp vegetation: environmental inferences. *International Journal of Coal Geology* **5**, 43–109.

Wnuk, C. and Pfefferkorn, H.W. (1987) A Pennsylvanian-age terrestrial storm deposit: using plant fossils to characterize the history and process of sediment accumulation. *Journal of Sedimentary Petrology* **57**, 212–221.

Ziegler, A.M. (1990) Phytogeographic patterns and continental configurations during the Permian Period. In: W.S. McKerrow and C.R. Scotese, eds. *Palaeozoic palaeogeography and biogeography*, pp. 363–379. Geological Society of London, Memoir no. 12.

1.3.9 Rise and Diversification of Insects

C.C. LABANDEIRA

Introduction

Insects are the most speciose group of macroscopic organisms ever to inhabit the planet. They are the major player in generating associations with microorganisms, fungi, and especially vascular plants; collectively these interacting groups contribute overwhelmingly to the bulk of community structure in land and freshwater ecosystems. The ecological dominance of insects also extends to estimates of biomass, abundance of individuals, and complexity of trophic webs, a condition probably present since the late Palaeozoic when global diversity estimates, as well as site-specific tabulations, indicate that insects were taxonomically the dominant terrestrial group (Labandeira and Sepkoski 1993), at least in lowland vegetated environments.

Origin and earliest fossil records of hexapods

The sparse fossil record of mid-Palaeozoic hexapods, the pattern of colonization of land by Palaeozoic plant and arthropod groups, and temporal constraints on hexapod origins imposed by hypotheses of arthropod phylogeny on hexapod origins all suggest that the earliest hexapods probably appeared during the Late Silurian. Although often used as a synonym for 'Insecta', the term 'Hexapoda' designates the more inclusive clade that consists of the Collembola (springtails) and Protura (proturans), collectively termed the Parainsecta, as well as its sister-group, the Insecta, which encompasses all other hexapods.

Early hexapod phylogeny

Phylogenetic evidence for the derivation of hexapods from another arthropod clade is still in an exploratory phase. Currently there are five major hypotheses of the origin of the Hexapoda (Fig. 1.3.9.1), but each is sufficiently unstable that differences in methodological approach, changes in included taxa or characters, and consideration of the fossil record can result in significant topological shifts within cladograms. This field is rapidly changing, and evidence linking the genetics and developmental biology of major arthropod clades is being used to test major phylogenetic schemes.

One of the oldest views of arthropod phylogeny is diphyly, with two superclades: the Schizoramia, consist-

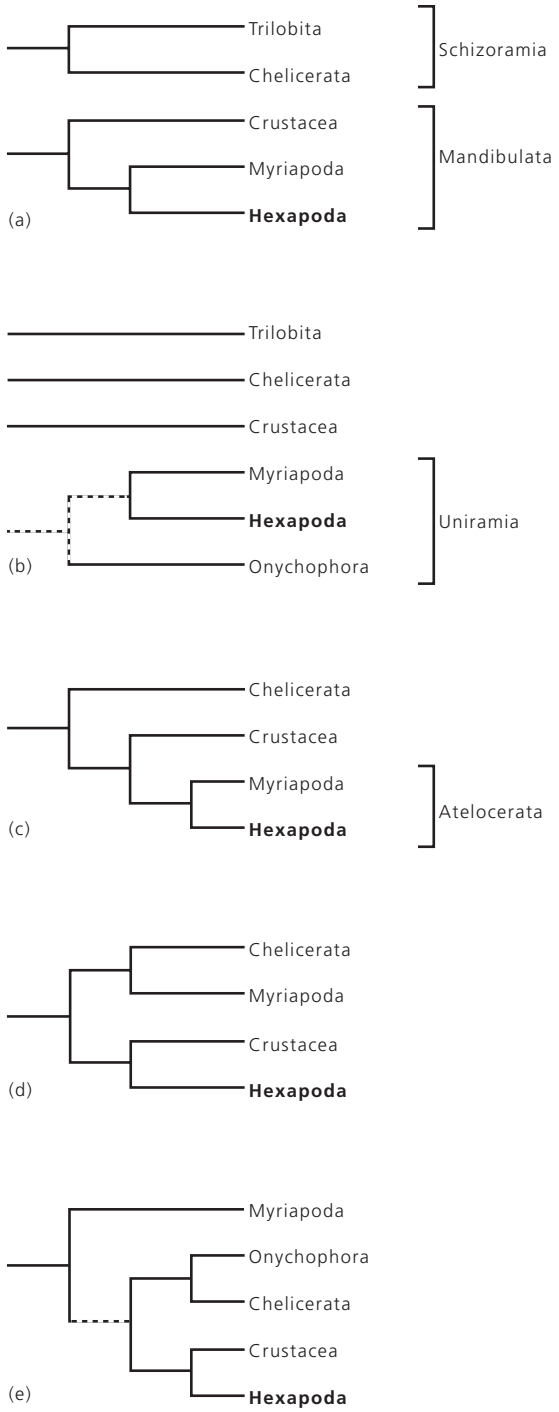


Fig. 1.3.9.1 Summaries of five hypotheses indicating the relationships of hexapods (in **bold**) to other major arthropod groups. (a) The hypothesis of arthropod diphyly, with Schizoramia and Mandibulata as distinct clades. (b) The hypothesis of extensive arthropod polyphyly, showing the traditional Uniramia as a distinct clade. (c) The hypothesis of arthropod monophyly, featuring the Mandibulata and its subgroup, the Atelocerata, as distinct clades. (d) One hypothesis of arthropod monophyly and a Crustacea + Hexapoda clade. (e) Another hypothesis of arthropod monophyly and a Crustacea + Hexapoda clade, with Onychophora included as arthropods. Branch lengths are arbitrary; dashed lines indicate nodes that are either theoretically inferred or not statistically valid. This is not an exhaustive list; see Fortey and Thomas (1997) for additional details.

ing of Chelicerata + Trilobita; and its sister-group, the Mandibulata, comprising the Crustacea and Hexapoda + Myriapoda (Fig. 1.3.9.1a). By contrast, Sydney Manton did not recognize these relationships, arguing instead for separate origins of the Trilobita, Crustacea, Chelicerata, and a Uniramia clade defined as Onychophora and Hexapoda + Myriapoda (Fig. 1.3.9.1b). Since her thesis was presented, arthropod polyphyly and the concept of the 'Uniramia' has largely been abandoned. Variations of two other major hypotheses receive most support from recent biomolecular and morphological studies. The first is the mandibulate/atelocerate hypothesis, consisting of a Crustacea and Hexapoda + Myriapoda clade that is a sister group to the Chelicerata, with or without inclusion of the Trilobita (Fig. 1.3.9.1c). The second, most recent, hypothesis posits a monophyletic Crustacea + Hexapoda clade that is a sister-group to other major arthropod clades, namely the Chelicerata + Myriapoda (Fig. 1.3.9.1d) or the Chelicerata + Onychophora with Myriapoda occurring as a basalmost clade (Fig. 1.3.9.1e). (See contributions in Fortey and Thomas (1997) for differing perspectives regarding the position of the Hexapoda within the Arthropoda.)

Within the Hexapoda, the position of the Parainsecta has always been controversial, particularly as the unique entognathous mouthparts and head sensory organs of the Collembola + Protura have frequently been cited as distinct from the Insecta. There is limited evidence that the Parainsecta may be separately derived from branchiopod crustaceans, a result that may explain why internal analyses of hexapods frequently result in an unresolved trichotomy involving the Parainsecta, the Diplura (which has variously been considered as parainsectan or insectan), and the Insecta. Nevertheless, the Insecta is generally regarded as monophyletic, and is united by several secure apomorphies. The most important evolutionary developments within the Insecta (Kukalová-Peck 1991; Fig. 1.3.9.2) were: (1) the transformation of the monocondylous mandible of the Archaeognatha into a robust mandible articulating with the head capsule by two condyles (Dicondylia); (2) the acquisition of wings (Pterygota); (3) the origin of holometabolous development (Holometabola), in which a larval stage became separated from its morpholo-

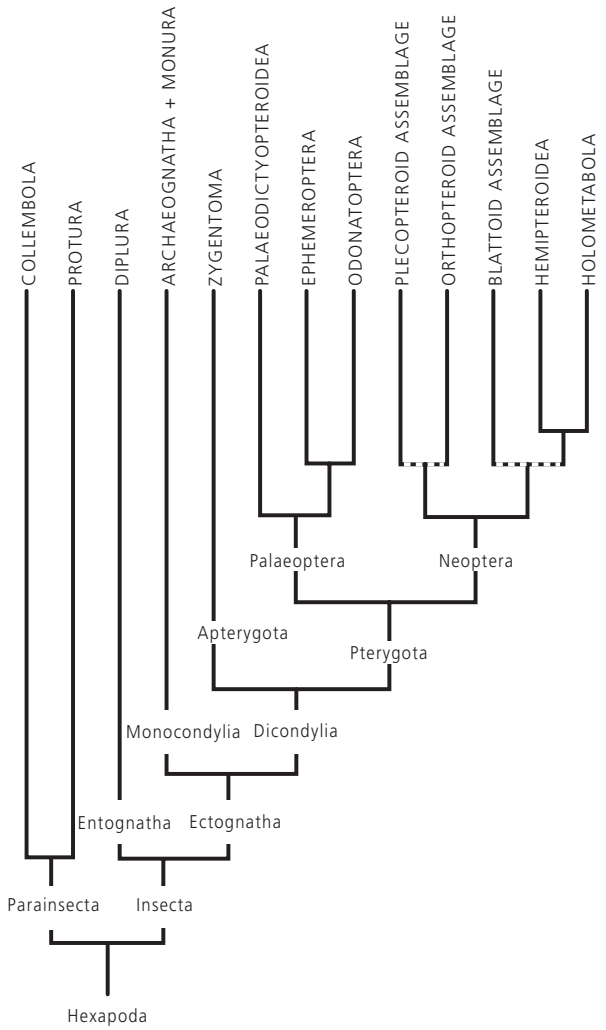


Fig. 1.3.9.2 Phylogeny of the major groups of hexapods, proposed by Kukalová-Peck (1991). Dashed lines indicate less secure relationships.

gically and ecologically distinct adult stage by a resting and non-feeding stage called the pupa; and (4) the invention of eusociality.

Devonian hexapods

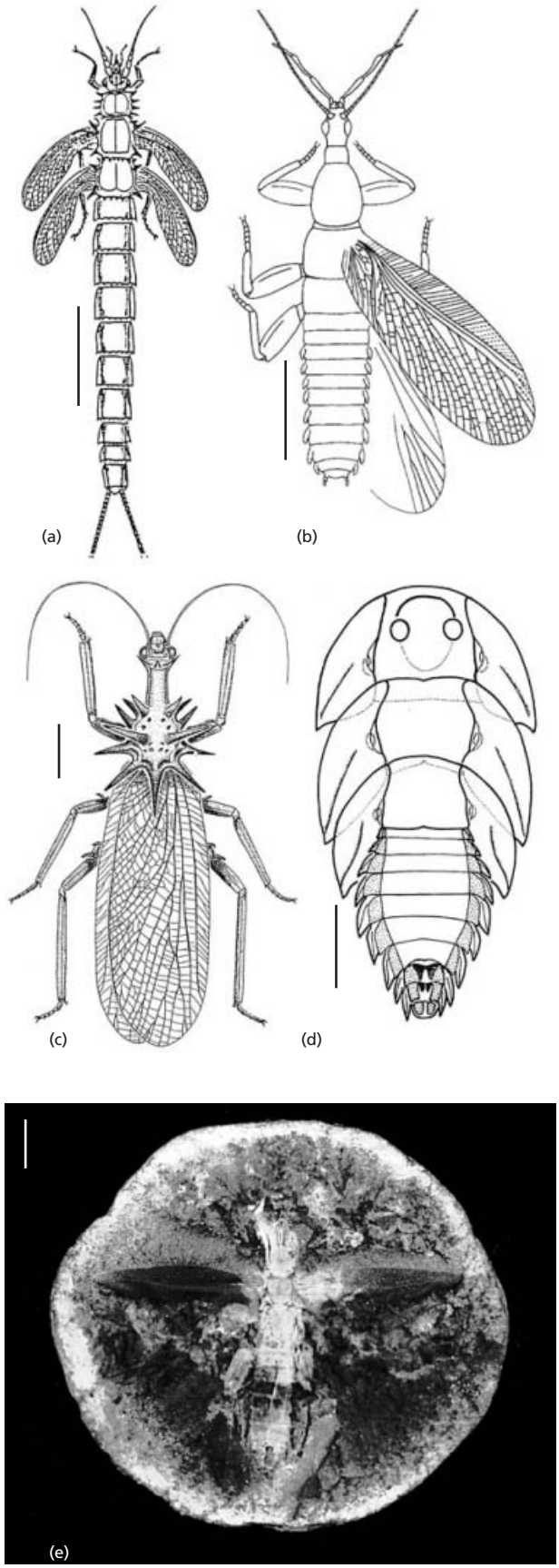
The earliest known hexapod is the springtail *Rhyniella* from the Rhynie chert of Scotland, of Early Devonian age, which occurs within a biota that includes primitive vascular plants and other arthropods, such as trigonotarbid spiders, mites, crustaceans, and myriapods (see Section 3.4.5). The earliest fossil insects are bristletails, known from a somewhat younger Early Devonian deposit from the Gaspé region of Quebec, Canada, and from the Middle Devonian of Gilboa, New York State. These earliest hexapod occurrences are unimpressive in diversity and abundance, presenting more questions than answers (Shear and Kukalová-Peck 1990). Hexapods are absent as fossils during a 55 million year interval from the Middle Devonian to the latest Early Carboniferous, during which time the major features of winged insects (Pterygota) must have evolved, based on the spectacular diversity of approximately 10 pterygote insect orders that appear suddenly at an interval straddling the Early to Late Carboniferous boundary (Brauckmann *et al.* 1995).

Insects in late Palaeozoic environments

During the early Late Carboniferous there was a dramatic appearance of diverse insect faunas at several major localities across equatorial Euramerica. A few middle Late Carboniferous to Early Permian localities yield faunas that are sufficiently diverse, abundant, and well preserved to have attracted considerable attention from palaeoentomologists. Two of the more notable insect fossil localities are in Illinois, USA. The first, Mazon Creek, is a celebrated body-fossil site in the north-central part of the state, of middle Late Carboniferous age. The second is the Calhoun Coal, a later Late Carboniferous trace-fossil deposit in the east-central region that provides a rare window into the associations of coal-swamp plants and their insects.

Late Carboniferous insects from an equatorial lowland

A relatively abundant assemblage of insects from Mazon Creek has been known for over 120 years (Carpenter 1997), consisting of approximately 175 known species, allocated to 38 families and 15 orders. This assemblage provides the earliest, well-documented glimpse of Palaeozoic insect life—inhabiting an emergent, equatorial landscape on a clastic delta that prograded southwesterly into a shallow epeiric sea. Insects from this deposit also originated from the 'uplands' surrounding this deltaic sedimentary wedge. Mazon Creek insects are preserved as moulds within flattened ovoidal concretions that are composed dominantly of siderite matrix, although the mineralized surfaces coating the entombed insects contain calcite, sphalerite, pyrite, kaolinite, and reduced iron oxides (Fig. 1.3.9.3e). These minerals were presumably formed in an anaerobic aquatic environment as insect carcasses were degraded by saprobic organisms that produced alkaline by-products resulting in early diagenetic mineralization. When carefully prepared, Mazon Creek insect fossils reveal considerable anatomical structure, such as minute venules and dark/light membrane patterns on wings. Other, typically preserved, features include sutures separating external body sclerites, cuticular ornamentation, spination, and the presence of delicate appendages such as



ovipositors, genitalia, abdominal exites, maxillary palpi, and antennae.

The major insect taxa recovered from Mazon Creek are typical of the Palaeozoic Insect Fauna, and are distinct at the highest taxonomic levels from the post-Permian Modern Insect Fauna, which consists overwhelmingly of familiar hemipteroid and holometabolous lineages that occur today. The fauna at Mazon Creek consists of the apterygote lineages Diplura (telsontails), Archaeognatha (bristletails), Monura, and Zygentoma (silverfish), as well as the pterygote lineages Protodonata (dragonflies), Palaeodictyoptera, Megasecoptera (Fig. 1.3.9.3a), Diaphanopterodea, Blattodea (cockroaches) (Fig. 1.3.9.3d), 'Protorthoptera' (Fig. 1.3.9.3b,c), Orthoptera (grasshopper-like insects), Caloneurodea, Hypoperlida (ancestral hemipteroids), Miomoptera, and probably Holometabola. Presumably the apterygote clades—those taxa primitively lacking wings—were generally detritivorous (Archaeognatha, Monura, Zygentoma) or probably predatory on other insects (Diplura). Clades of Pterygota that were primitively unable to flex their wings over their abdomen were large to gigantic in size, and were either top aerial predators (Protodonata) or had stylate mouthparts (Palaeodictyopteroidea) involved in piercing-and-sucking of plant tissues (Labandeira 1997). Mandibulate orthopteroid taxa, mostly the polyphyletic and varied 'Protorthoptera', but also oedischiid Orthoptera, may have been either detritivores or herbivorous consumers of plant foliage. By contrast, early members of the hemipteroid assemblage (Caloneurodea, Hypoperlida) bore mouthpart structures presaging those of Permian Hemiptera, including styliform mouthpart elements and a domed clypeal pump indicating imbibation of plant fluids or small particles such as spores. The enigmatic Miomoptera are considered holometabolous by some, although there is stronger evidence for the presence of early Holometabola with the recent discovery of a caterpillar-like larva (Kukalová-Peck 1991). If this assignment is true—and there is additional evidence for the presence of Holometabola from plant damage in a slightly

Fig. 1.3.9.3 A representative sample of Mazon Creek insects, from the middle Late Carboniferous of Illinois, USA. (a) Nymph of *Mischoptera douglassi* (Megasecoptera: Mischopteridae). (b) Adult of *Eucaenus ovalis* ('Protorthoptera': Eucaenidae). (c) Adult of *Gerarus danielsi* ('Protorthoptera': Geraridae). (d) Undetermined cockroach nymph, ventral view. (e) Siderite concretion of an unnamed eucaenid protorthopteran. Scale bars = 1 cm. (b, From Carpenter 1997, reproduced with permission of Northeastern Illinois University Press; a,c,d, from Kukalová -Peck 1991, reproduced with permission of Cornell University Press.)

younger Late Carboniferous deposit (Labandeira 1998)—then this diverse assemblage embodies three major evolutionary events that characterized the history of the Insecta (see above), with the exception of the origin of eusociality during the Early Cretaceous.

A Late Carboniferous community of insects on a tree fern

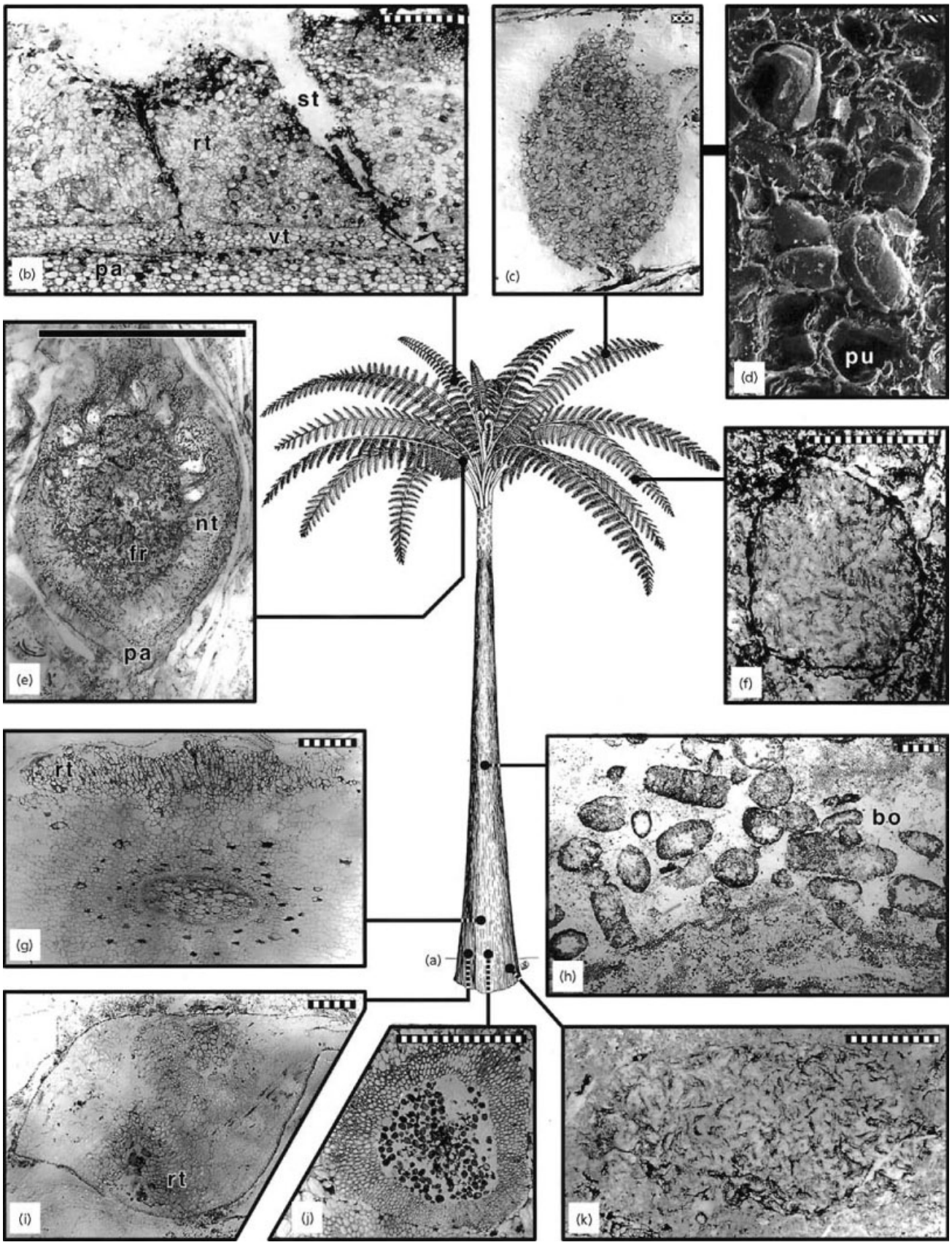
Virtually all understanding of Palaeozoic insects is based on their external morphologies and intragroup and intergroup taxonomic relationships. The ecological associations of Palaeozoic insects with other organisms, and their trophic roles in terrestrial ecosystems, are a more recent focus of research. The best-studied deposit for assessing Palaeozoic insect palaeoecology is the Calhoun Coal of the Mattoon Formation. Within this coal unit there are permineralized nodular structures that preserve swamp plants in exceptional anatomical detail, including cellular detail of tissues and the histological structure of organs, principally from the marattialean tree fern *Psaronius* and the seed fern *Medullosa*. Tissue damage patterns in these two arborescent plants provide a clear picture of how insect herbivores and detritivores trophically partitioned plant organs and reveal the spectrum of insect functional feeding groups that was present during the Late Carboniferous (Labandeira 1998).

At least seven distinctive insect functional feeding groups have been documented for *Psaronius* (Fig. 1.3.9.4a), collectively representing a community of consumers trophically dependent on a plant host, each using a stereotyped mode of feeding to target a particular tissue (Labandeira 1998). Mandibulate insects representing canopy herbivores fed externally on most foliar tissues (Fig. 1.3.9.4f); other mandibulate insects tapped sporangia collectively or spores individually for selective ingestion (Fig. 1.3.9.4c,d); a palaeodictyopteran insect with stylate mouthparts consumed xylem and phloem of petiolar vascular tissue by piercing and sucking (Fig. 1.3.9.4b); and a holometabolous larva encapsulated in petiolar inner parenchyma elicited a reciprocal host-plant response through galling (Fig. 1.3.9.4e). Evidence also indicates that this insect galler induced proliferation of a distinctive response tissue from *Psaronius* (Fig. 1.3.9.4e) and was targeting the basal frond petioles of only this species, indicating an intimate and host-specific association. Within the trunk and root system of *Psaronius*, three types of endophytic borers are known: an unknown herbivorous insect borer of parenchyma within exposed roots (Fig. 1.3.9.4i,k), and two detritivorous borers—a stem borer of soft parenchyma located between more indurated trunk tissues (ecologically analogous to certain modern cockroaches) (Fig. 1.3.9.4h), and a mite on the hard supportive tissue of the root mantle (Fig. 1.3.9.4j). Lastly there was an external grazer on root epidermis (Fig. 1.3.9.4g). With the exception of leaf mining, the earliest occurrence of which is Middle Triassic, the coarse spectrum of herbivore and detritivore functional feeding groups in this Carboniferous community is remarkably complete and modern, although the post-Palaeozoic counterparts of these feeding types were occupied by entirely different taxa.

Post-Palaeozoic developments

During the Permian there was gradual supplementation of typical Late Carboniferous insect taxa by basal

Fig. 1.3.9.4 (*Facing page*) The community of insect herbivores and detritivores on their late Pennsylvanian (300 Ma) host plant, *Psaronius*, a tree fern that dominated peat-substrate swamp forests of the Illinois Basin. Members of the *Psaronius* component community are inferred from patterns of host-plant tissue damage and associated coprolite contents. All interactions are from insects, except (j) which is a mite. Most of these associations indicate feeding on live plant tissue (herbivory) and are confined to the canopy or exposed roots at ground level; however, interactions indicated by (h), (j), and probably (k) are examples of detritivory. (a) Reconstruction of *Psaronius chasei* Morgan, a marattialean tree fern approximately 10 m tall, from the Mattoon Formation (Calhoun Coal) of the Illinois Basin. (b) Stylet tracks in a frond-bearing petiole, showing that vascular tissue (xylem and phloem) was being targeted by a piercing-and-sucking palaeodictyopterid insect. (c) Insect coprolite occurring in peat litter, consisting almost entirely of *Punctatisporites* spores from a *Psaronius* source plant. (d) SEM enlargement of section in (c) showing crushed and relatively intact spores that have passed through an insect's gut. (e) Gall from a frond petiole, showing a tunnelled centre replaced by insect frass, surrounded by a zone of nutritive tissue proliferation and normal outer parenchyma; the galler is a holometabolous insect. (f) Another coprolite from peat litter, containing leaf cuticle and trichomes borne by *Psaronius* foliage. (g) Surface grazing on a ground-level root, characterized by files of abnormally produced cells of reaction tissue. (h) An insect boring of stem tissue within the central trunk, displaying consumption of softer parenchyma but avoidance of more indurated root mantle, sclerenchyma, and vascular strands (outer root mantle is toward the bottom; inner stem tissues are at the top). (i) A boring of a surface root, showing a chamber filled with coprolites, surrounded by tufts of reaction tissue. (j) An example of mite consumption of woody tissue along the outer root mantle, indicated by very small coprolites occurring in the lumen of a mantle root. (k) An elongate coprolite wedged in peat litter, showing a distinctive texture of collapsed root epidermis, indicating consumption of a ground-level root. Abbreviations: bo, stem boring; fr, insect-associated frass; nt, gall-produced nutritive tissue; pa, parenchyma; pu, *Punctatisporites* spores as gut contents; rt, reaction tissue; st, stylet trace piercing outer parenchyma tissue; vt, vascular tissue (xylem). Scale bars: solid = 1.0 cm; striped = 0.1 cm; dotted = 0.01 cm; backslashed = 0.001 m.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lineages of hemipteroid and holometabolous insects. Although Late Permian insect faunas are poorly known, it is clear that the terminal Permian extinction had a profound effect on the course of insect evolution by extirpating most of the major Palaeozoic lineages. Those that survived into the Triassic were preferentially enriched in hemipteroid and holometabolous taxa. The spectrum of insect taxa from Late Triassic faunas is fundamentally modern in composition, containing few Palaeozoic lineages (Labandeira and Sepkoski 1993; Anderson *et al.* 1998). Importantly, this Modern Insect Fauna represents a separate macroevolutionary radiation into the same ecological roles previously occupied by the Palaeozoic Insect Fauna (Labandeira 1997).

During the preangiospermous Mesozoic, freshwater habitats were invaded by several insect clades, particularly Diptera (flies) and Trichoptera (caddisflies). Meanwhile, the diversification of many seed-plant lineages on land, such as conifers, seed ferns, cycads, bennettitaleans, and ephedraleans, resulted in a proliferation of associations with insects, including external feeders such as chrysomelid beetles, endophytic gallers, and leaf miners, in addition to pollination mutualisms such as those between cycads and weevils that persist today. The appearance of angiosperms during the Early Cretaceous offered new and diverse substrates for dietary partitioning (Labandeira 1997; Wilf *et al*. 2000), even though major feeding adaptations had occurred earlier on other seed-plant lineages. Later events of importance for insect evolution included the extensive diversification of placental mammals during the early Cenozoic, which offered new opportunities for colonization by endoparasitic and ectoparasitic insects, and the geographical spread of the grassland biome during the mid-Cenozoic, which induced specialization by numerous herbivorous insect lineages.

References

Anderson, J.M., Anderson, H.M. and Cruickshank, A.R.I. (1998) Late Triassic ecosystems of the Molteno/Lower Elliot biome of southern Africa. *Palaeontology* **41**, 387–421.

Brauckmann, C., Brauckmann, B. and Gröning, E. (1995) The stratigraphical position of the oldest known Pterygota (Insecta, Carboniferous, Namurian). *Annales de la Société Geologique de Belgique* **117**, 47–56.

Carpenter, F.M. (1997) Insecta. In: C.W. Shabica and A.A. Hay, eds. *Richardson's guide to the fossil fauna of Mazon Creek*, pp. 184–193. Northeastern Illinois University Press, Chicago.

Fortey, R.A. and Thomas, R.H., eds. (1997) *Arthropod relationships*. Systematics Association Special Volume, no. 55. Chapman and Hall, London.

Kukalová-Peck, J. (1991) Fossil history and the evolution of hexapod structures. In: I.D. Naumann, P.B. Carne, J.F. Lawrence, E.S. Nielsen, J.P. Spradbery, R.W. Taylor, M.J. Whitten and M.J. Littlejohn, eds. *Insects of Australia*, 2nd edn, pp. 141–179. Cornell University Press, Ithaca, New York.

Labandeira, C.C. (1997) Insect mouthparts: ascertaining the paleobiology of insect feeding strategies. *Annual Review of Ecology and Systematics* **28**, 153–193.

Labandeira, C.C. (1998) Early history of arthropod and vascular plant associations. *Annual Review of Earth and Planetary Sciences* **26**, 329–377.

Labandeira, C.C. and Sepkoski, J.J. Jr (1993) Insect diversity in the fossil record. *Science* **261**, 310–315.

Shear, W.A. and Kukalová-Peck, J. (1990) The ecology of Paleozoic terrestrial arthropods: the fossil evidence. *Canadian Journal of Zoology* **68**, 1807–1834.

Wilf, P., Labandeira, C.C., Kress, W.J., Staines, C.L., Windsor, D.M., Allen., A.L. and Johnson, K.R. (2000) Timing the radiations of leaf beetles: hispines on gingers from latest Cretaceous to Recent. *Science* **289**, 291–294.

1.3.10 Origin of Mammals

J.A. HOPSON

Introduction

Mammals have been major components of terrestrial and aquatic environments for only the past 65 million years, even though the first mammal, defined as the common ancestor of the living monotremes, marsupials, and placentals, appears to have lived some 150 million years earlier, during the Late Triassic. More distant antecedents of mammals, the non-mammalian synapsids or 'mammal-like reptiles', can be traced back an additional 100 million years, to the Late Carboniferous, when Synapsida and Sauropsida (the clade that includes living reptiles and birds) diverged.

The fossil record of synapsids is remarkable for its completeness in documenting the gradual evolutionary transition from ectothermic basal synapsids, or 'pelycosaurs', to fully endothermic mammals (Kemp 1982; Hopson 1994; Sidor and Hopson 1998). Synapsid diversification (Fig. 1.3.10.1) can be regarded as a series of adaptive radiations, each structurally closer to modern mammals: the Late Carboniferous–Early Permian pelycosaurs; the primarily Late Permian non-cynodont therapsids; the primarily Triassic non-mammalian cynodonts; the Late Triassic–Late Cretaceous basal mammals (non-therian mammaliaforms); and the Late Cretaceous–Recent therians (marsupials and placentals).

Interestingly, each of these radiations includes at least one long-surviving group that coexisted for a time with the succeeding, more mammal-like radiation. These long-lived taxa—caseid pelycosaurs, anomodont therapsids, tritylodontid cynodonts, and multituberculate mammals—were all herbivores whose survival may

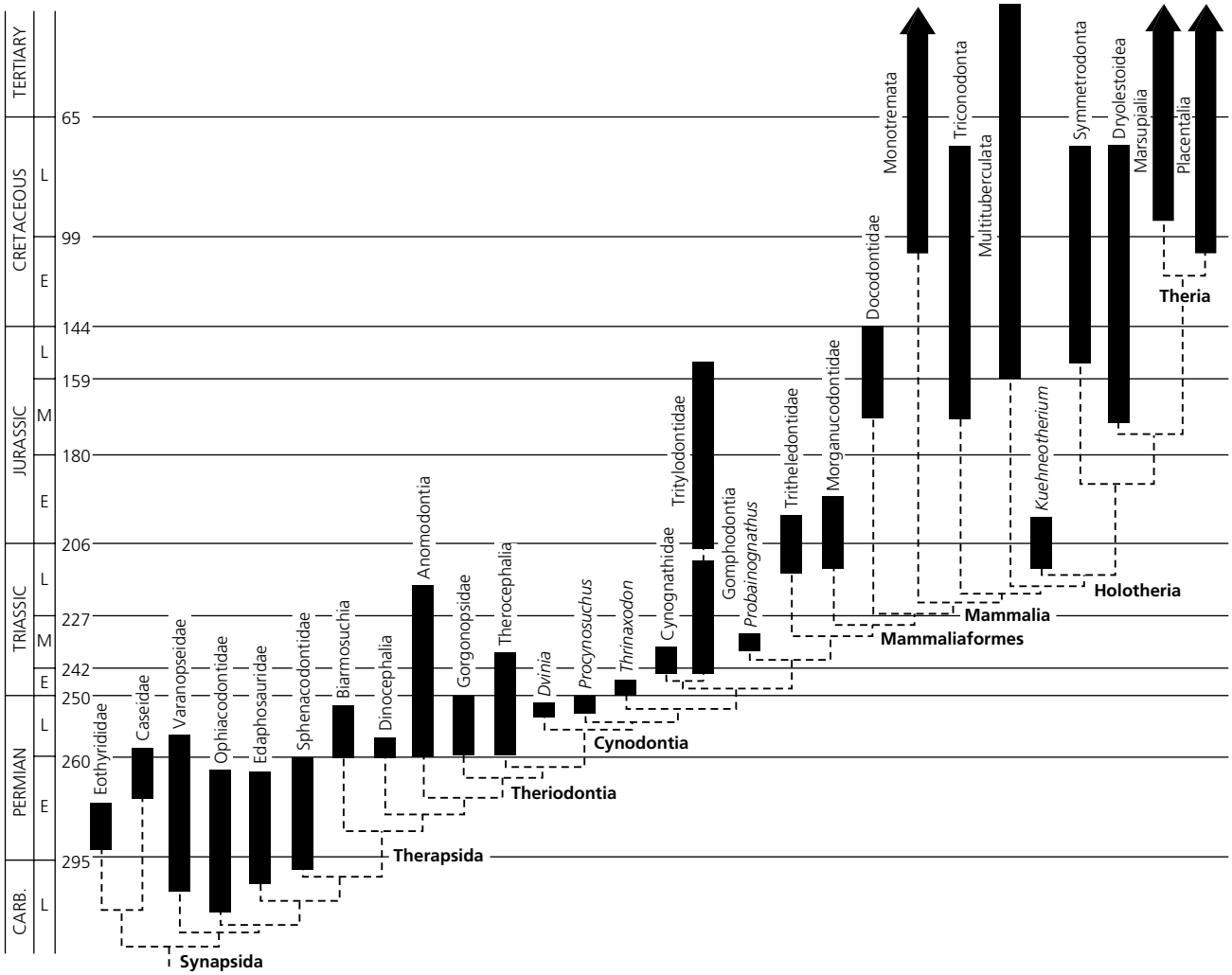

Fig. 1.3.10.1 Phylogenetic diagram of the major clades of Synapsida ('mammal-like reptiles' and mammals) on a geological time scale. Vertical bars indicate known taxon ranges. The ranges of Monotremata, Marsupialia, and Placentalia extend to the present. Divergence times of sister taxa, indicated by dashed lines, are hypothetical. Basal (non-therapsid) synapsids form a paraphyletic group informally called 'pelycosaurs'. Tritylodontidae is a terminal subgroup of Gomphodontia. Triconodonta, Multituberculata, and Holotheria form the Theriimorpha.

be explained by specialized trophic adaptations that allowed them to successfully compete with their more physiologically mammalian contemporaries. This also applies to the highly specialized invertebrate-eating monotremes, the only non-therian mammals to survive beyond the Eocene.

Comparison of basal synapsids with mammals

The magnitude of the differences in anatomy and physiology between a basal synapsid and a primitive living mammal may be inferred from an examination of their skulls (Hopson 1994). The pelycosaur (Fig. 1.3.10.2a) was an ectotherm, as are living reptiles, with a resting metabolic rate too low to generate sufficient heat to warm its body above ambient temperature. Therefore, its food and oxygen requirements were about one-tenth those of a mammal of comparable size. This is reflected in the simple dentition, adapted for capturing and holding prey items but not for breaking them down into small bits. Also, the internal nostrils, or choanae, lie near the front of the mouth, so that air had to traverse the oral cavity to deliver oxygen to the lungs; if food blocked the air passage, the animal was able to suspend breathing for a few minutes without ill effect.

Synapsid skulls are characterized by an opening behind the eye, the temporal fenestra, which in pelycosaurs is relatively small. An undifferentiated mass of jaw-closing muscles was restricted to the small space beneath the cheek, attaching primarily to the underside of the broad skull roof. As in all other non-mammalian tetrapods, the lower jaw of the basal synapsid consists of

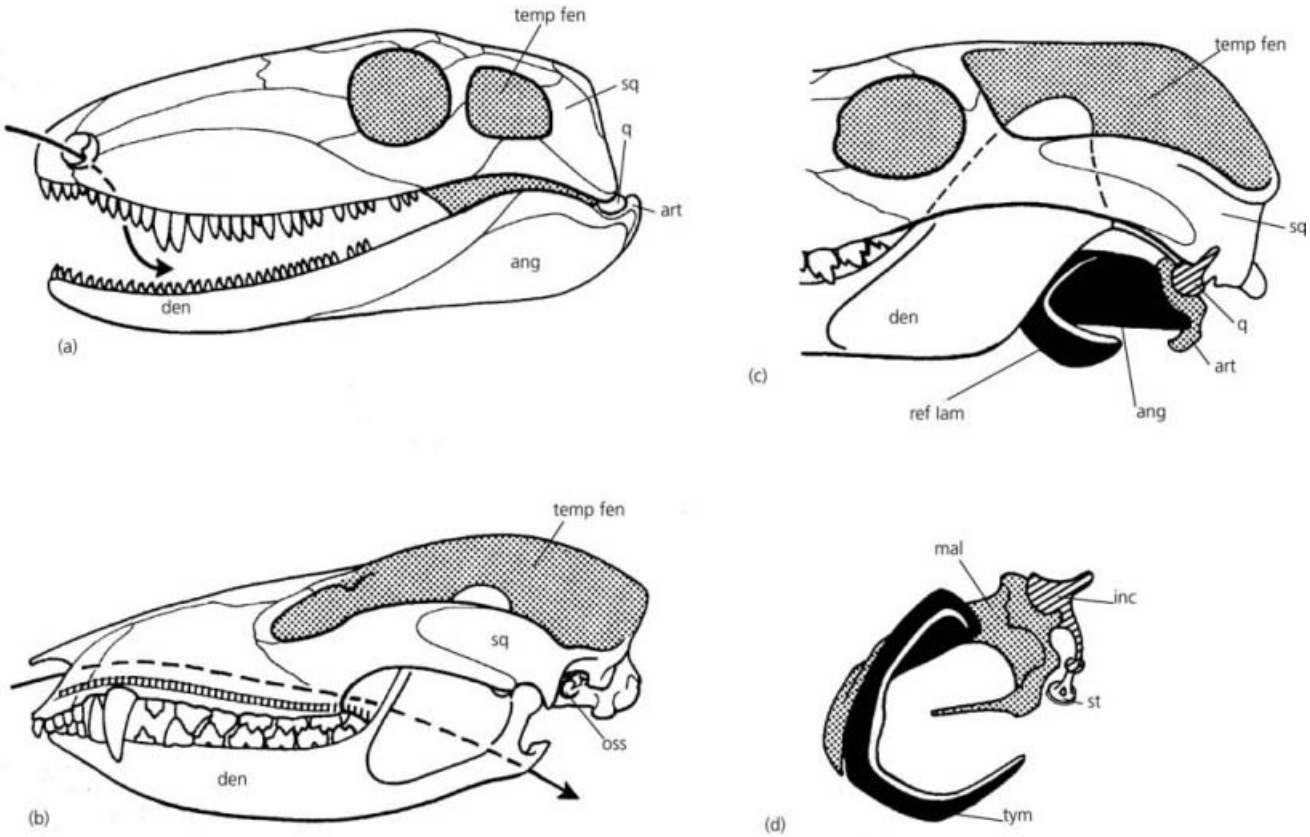

Fig. 1.3.10.2 Skulls of (a) an Early Permian basal synapsid, or 'pelycosaur' (based on the ophiacodontid *Varanosaurus*), and (b) a Recent mammal, the Virginia opossum (*Didelphis virginianus*), to show the craniodental differences between an ectothermic and an endothermic synapsid. Arrows indicate the path of inspired air; vertical hatching in (b) indicates the bony secondary palate. (c) Posterior half of the skull of an Early Triassic cynodont (*Thrinaxodon*). (d) Middle ear ossicles of a mammal (*Didelphis*). Patterning in (c) and (d) indicates homologous elements in the cynodont jaw and the mammalian middle ear. The eardrum of the mammal is held by the C-shaped tympanic bone; possibly the hook-like reflected lamina of the Triassic cynodont also held a tympanum in life. Abbreviations: ang, angular; art, articular; den, dentary; inc, incus; mal, malleus; oss, middle ear ossicles; q, quadrate; ref lam, reflected lamina; sq, squamosal; st, stapes; temp fen, temporal fenestra; tym, tympanic. (From Hopson 1994.)

a large number of bones behind the tooth-bearing dentary, with an articular bone forming a hinge-like jaw joint with the quadrate bone in the skull.

The opossum (Fig. 1.3.10.2b), like all mammals, is an endotherm, with an active metabolism generating sufficient heat to provide a constant high optimal body temperature, irrespective of ambient temperature. The mammalian dentition is differentiated into pointed incisors and canines in front for grasping and killing prey, and premolars and molars behind for breaking it down; this vastly increases the surface area available to digestive enzymes and thus increases the rate at which food energy is assimilated. The choanae no longer open directly into the mouth; rather, the air passage is separated from the oral cavity by a bony plate, the secondary palate. Thus, mammals have evolved special features for the rapid delivery of food energy and the uninterrupted delivery of oxygen to their body tissues, in order to maintain an endothermic metabolism.

The jaw muscles of mammals have increased both in mass and complexity, with one portion, the temporalis, attaching around the margins of a greatly enlarged temporal fenestra (now confluent with the eye socket) and a new external portion, the masseter, attached to the cheek bone (zygomatic arch). The lower jaw is formed entirely by the dentary, which bears a posterodorsal coronoid process for attachment of the temporalis and a posteroventral angular process for attachment of the masseter. These muscles aid in moving the lower jaw from side to side so that the molars can effectively slice and grind the food.

The mammalian jaw joint is a new structure, formed by the dentary with the squamosal bone of the skull. The quadrate and certain postdentary bones of the synapsid

lower jaw have been shifted into the middle ear (Fig. 1.3.10.2c,d) where they serve to transmit sound vibrations from the eardrum to the inner ear (Allin and Hopson 1992).

Comparison of the postcranial skeleton of early synapsids with that of mammals also permits inferences about differing activity levels. Pelycosaurs have relatively short sprawling limbs, with joint surfaces permitting only a restricted range of movements. Lateral bending of the trunk helped to increase stride length, but such side-to-side movement also interfered with ventilation of the lungs (Carrier 1987). Thus, pelycosaurs, like living reptiles, probably suspended breathing while running, relying on anaerobic muscle metabolism to sustain a short burst of speed. In contrast, mammals have a more upright stance and more mobile limb joints, permitting the long limbs to move with greater freedom in a fore–aft plane. The trunk bends in a dorsoventral plane, which both increases stride length and aids in ventilating the lungs. Thus, mammals increase respiratory rate with increasing speed and so are able to sustain high levels of aerobic activity over long periods of time.

Basal synapsids—'pelycosaurs'

The earliest undoubted synapsids are known from Late Carboniferous rocks, about 310 Ma. By the end of the Carboniferous, all major pelycosaur groups must have been in existence, though caseasaurs are first known from the Early Permian (Fig. 1.3.10.1). Pelycosaurs are extremely abundant in the Early Permian of North America and western Europe, diversifying into small to medium-sized hunters of arthropods and other small animals (eothyridids and varanopseids), large predators on vertebrates (ophiacodontids and sphenacodontids), and some of the earliest obligate herbivores among terrestrial vertebrates (edaphosaurids and caseids). Among pelycosaur-grade synapsids, only caseids and varanopseids survived into the early Late Permian to coexist with basal therapsids.

Sphenacodontids, which include the well-known 'sailback' *Dimetrodon*, as well as sail-less taxa, share many features with their more derived sister group, the Therapsida. Notably, they have enlarged canine teeth and a posteriorly notched keel on the angular bone of the lower jaw; this reflected lamina of the angular (Fig. 1.3.10.3a) provides the first hint of the mammalian tympanic bone.

Because of their sprawling posture and use of lateral undulation of the trunk in locomotion, pelycosaurs, like many living reptiles, probably ambushed prey, capturing them after a short dash fuelled by anaerobic muscle activity.

Therapsids

The earliest therapsids, known from the Kazanian of Russia, South Africa, and possibly China, belong to three major groups: Biarmosuchia, Dinocephalia, and Anomodontia. A fourth group, the Theriodontia, appears in slightly younger faunas. Biarmosuchians are very sphenacodontid-like in retaining a small temporal fenestra, though a slip of jaw musculature passed out through the fenestra to attach on its outer margin (Fig. 1.3.10.3b). The upper canine is very long and the reflected lamina of the angular is deeply emarginated. Dinocephalians and anomodonts have larger temporal fenestrae, with a greater mass of musculature attaching to the outer surfaces of surrounding bones.

Therapsids differ from pelycosaurs in having a more upright stance, with the limbs held closer to the body. The limb joints permitted greater freedom of movement and lateral undulation of the trunk was probably reduced. The changes in the locomotor apparatus suggest that therapsids may have actively foraged for food over much greater distances than was possible for pelycosaurs; this change in hunting behaviour would have selected for an increased ability of the respiratory and cardiovascular systems to sustain aerobic activity. Ultimately, selection for increased aerobic capacity led to the elevated metabolic rates associated with mammalian endothermy (Bennett and Ruben 1979).

The main predators of the Late Permian were the theriodonts, characterized by large serrated canines, a low skull with a large temporal opening, and a coronoid process on the dentary. Theriodonts include the primitive gorgonopsians (Fig. 1.3.10.3c), with a broad temporal roof, and the more derived therocephalians and cynodonts, grouped as eutheriodonts, in which the temporal fenestra is expanded medially to leave only a narrow roof, with a sagittal crest for muscle attachment. Therocephalians were a diverse group, including large predators and small, lightly built, insectivores; among the latter, Early Triassic bauriids paralleled cynodonts in developing expanded, occluding teeth and a secondary palate.

The earliest cynodonts, of very late Permian age, are *Dvinia* from Russia and *Procynosuchus* (Fig. 1.3.10.3d) from Germany and Africa, the latter corresponding closely to the common ancestor of all later cynodonts, including mammals. Their postcanine teeth have accessory cusps that give them a molar-like appearance. The zygomatic arches are flared out from the lower jaw, creating a gap through which a slip of undifferentiated jaw muscle, an incipient masseter, shifted to the outer surface of the coronoid process. In the palate, a pair of bony plates extends medially to form a partial secondary palate separating the air passage from the mouth. These specializations indicate that cynodonts were breaking

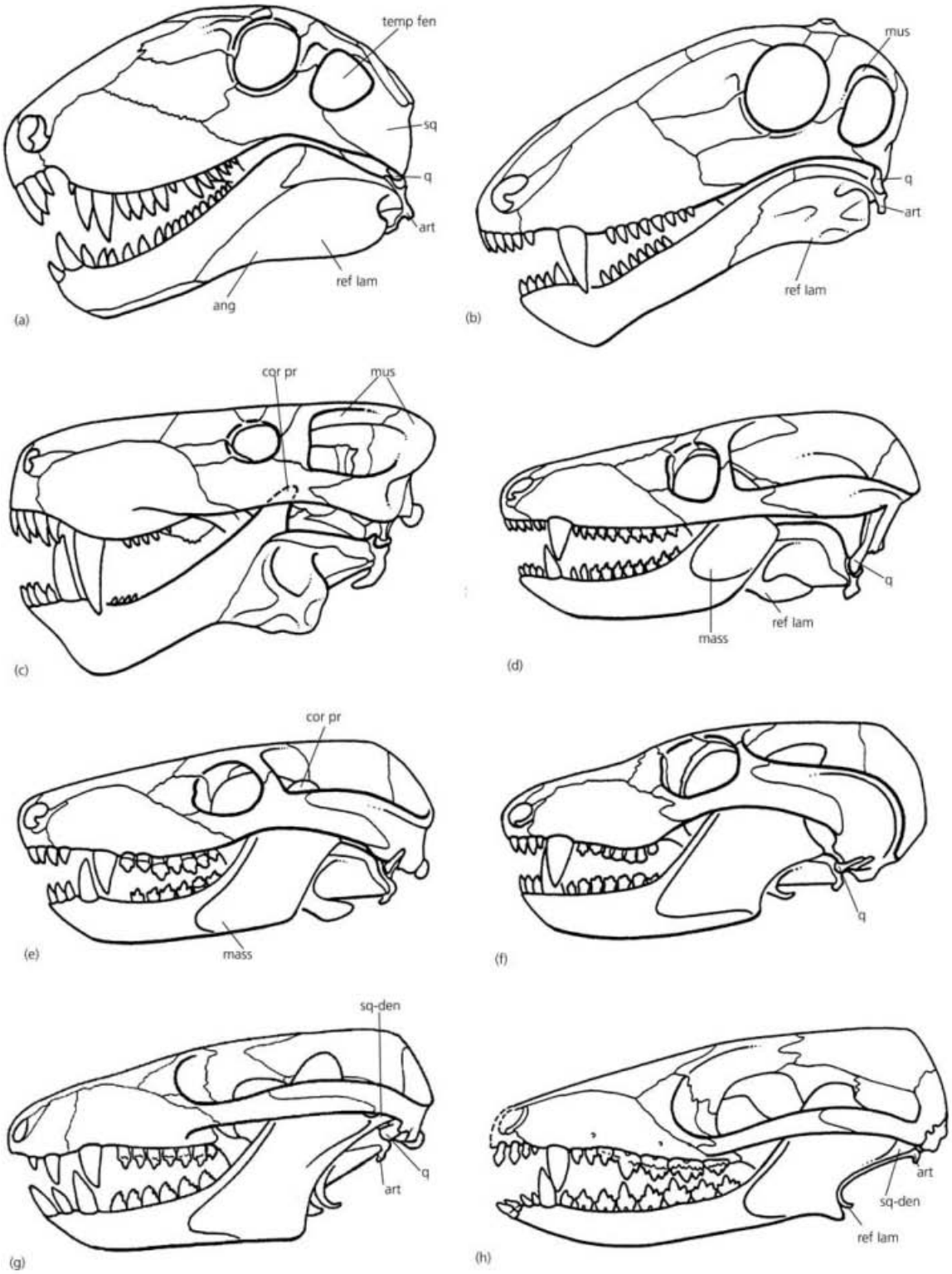

Fig. 1.3.10.3 Skulls of synapsids. (a) Sphenacodontid 'pelycosaur' *Dimetrodon*. (b) Basal therapsid *Biarmosuchus*. (c) Gorgonopsian *Leontocephalus*. (d) Late Permian cynodont *Procynosuchus*. (e) Early Triassic cynodont *Thrinaxodon*. (f) Middle Triassic cynodont *Probainognathus*. (g) Tritheledontid cynodont *Pachygenelus*. (h) Early mammaliaform *Morganucodon*. Abbreviations: cor pr, coronoid process; mass, area of attachment of masseter muscle; mus, muscle attachment site; sq-den, squamosal–dentary jaw contact. Other abbreviations as in Fig. 1.3.10.2. (From Hopson 1994.)

down food orally without interrupting the flow of oxygen to the lungs, features suggesting a more endothermic physiology than occurred in earlier therapsids.

Triassic cynodonts bridge the gap to mammals. The Early Triassic *Thrinaxodon* (Figs 1.3.10.2c, 1.3.10.3e) further enlarged the dentary and reduced the postdentary elements, including the reflected lamina. A fully developed masseter extended to the lower border of the jaw and a differentiated temporalis attached to a robust coronoid process. The cheek teeth are more complex, resembling those of early mammals, and the palatal plates join on the midline to form a complete secondary palate. In the Middle Triassic, more derived cynodonts, such as *Probainognathus* (Fig. 1.3.10.3f), have postdentary bones reduced to a slender rod and a large dentary closely approaching, though not contacting, the skull. This contact is seen in tritheledontid cynodonts, such as *Pachygenelus* (Fig. 1.3.10.3g), and near-mammals, such as *Morganucodon* (Fig. 1.3.10.3h), from the Late Triassic/Early Jurassic. In the latter, the rear of the dentary forms a knob, or condyle, which fits into a hollow, or glenoid, on the squamosal.

The postdentary bones of Triassic cynodonts show progressive reduction to a slender rod, with the reflected lamina becoming a delicate hook. The articular and quadrate are also reduced in size and the whole apparatus takes on the appearance of mammalian middle ear bones, though how it functioned is uncertain. Possibly the reflected lamina supported an eardrum, the vibrations of which caused the postdentary rod to move, thus conducting sound vibrations from the articular to the quadrate and thence, via the stapes (the reptilian ear bone), to the inner ear (Allin and Hopson 1992). Once the dentary contacted the skull and the new mammalian jaw joint took over, the postdentary sound-conducting apparatus was free to relinquish its dentary attachment and become firmly joined to the ear region of the skull. Fossil evidence indicates that separation of the ear ossicles from the dentary occurred independently in several groups of early mammals.

Mammaliaforms and mammals

The earliest true mammals are known from the Late Triassic (Norian), about 210 Ma. Appearing somewhat earlier are what might be called near-mammals, creatures which in life probably looked like mammals but which lie phylogenetically outside the Mammalia as currently defined (the common ancestor of monotremes, marsupials, and placentals and its descendants; McKenna and Bell 1997). The near-mammals are placed in a more inclusive taxon Mammaliaformes, which includes Mammalia plus the Late Triassic/Early Jurassic *Morganucodon* and related forms, as well as the Middle–Late Jurassic docodonts. Mammaliaforms are characterized by having molars with two roots and precise occlusion between matching shear surfaces on upper and lower teeth. Their molars are no longer replaced and the more anterior teeth have a single milk series that is replaced by a set of permanent teeth; limited replacement appears to be correlated with precise occlusion and contrasts with the unlimited replacement in the non-occluding teeth of earlier synapsids. Although basal mammaliaforms possess a dentary–squamosal jaw joint, they retain a functional articular–quadrate joint beside it.

Also known from the Late Triassic is *Kuehneotherium*, the earliest member of the Holotheria, the group including the living marsupials and placentals. Holotheres are characterized by molars in which the three main cusps, rather than lying in a fore–aft line (as in *Thrinaxodon* or *Morganucodon*), form a broad V, the apex of which points inward in the uppers and outward in the lowers; thus, the tooth rows form a zigzagging cutting surface. On this 'reversed triangles' molar pattern was based the enormous functional diversity seen in the molars of therian mammals.

Though not known with certainty prior to the Middle Jurassic, the other major mammalian clades—monotremes, triconodonts, and multituberculates—must have diverged from their common ancestor with the holotheres some time in the Late Triassic. The phylogenetic relationships of the egg-laying monotremes (the living platypus and echidnas of the Australian region) have long been a mystery because of their extremely specialized skulls, cynodont-like postcranial skeletons, and lack of adult teeth. Fossil monotreme teeth from the Early Cretaceous of Australia have suggested a special relationship with Late Jurassic holotheres (Kielan-Jaworowska *et al.* 1987). However, recent discoveries of complete triconodont, multituberculate, and basal holothere (symmetrodont) specimens demonstrate that these taxa all possess postcranial skeletons strikingly similar to those of living therians and much more derived than the Triassic-grade skeletons of living monotremes (Hu *et al.* 1997). Thus, triconodonts (Middle Jurassic–Late Cretaceous carnivores with blade-like molars) and multituberculates (Late Jurassic–Late Eocene rodent-like herbivores) form a clade with holotheres, the Theriimorpha, from which monotremes are excluded.

References

Allin, E.F. and Hopson, J.A. (1992) Evolution of the auditory system in Synapsida ('mammal-like reptiles' and primitive mammals) as seen in the fossil record. In: D.B. Webster, R.R. Fay and A.N. Popper, eds. *The evolutionary biology of hearing*, pp. 587–614. Springer-Verlag, New York.

Bennett, A.F. and Ruben, J.A. (1979) Endothermy and activity in vertebrates. *Science* **206**, 649–654.

Carrier, D.R. (1987) The evolution of locomotor stamina in tetrapods: circumventing a mechanical constraint. *Paleobiology* **13**, 326–341.
Hopson, J.A. (1994) Synapsid evolution and the radiation of non-eutherian mammals. In: D.R. Prothero and R.M. Schoch, eds. *Major features of vertebrate evolution*, pp. 190–219. Short Courses in Paleontology, no. 7. University of Tennessee, Knoxville.
Hu, Y., Wang, Y., Luo, Z. and Li, C. (1997) A new symmetrodont mammal from China and its implications for mammalian evolution. *Nature* **390**, 137–142.
Kemp, T.S. (1982) *Mammal-like reptiles and the origin of mammals*. Academic Press, London.
Kielan-Jaworowska, Z., Crompton, A.W. and Jenkins, F.A. Jr (1987) The origin of egg-laying mammals. *Nature* **326**, 871–873.
McKenna, M.C. and Bell, S.K. (1997) *Classification of mammals above the species level*. Columbia University Press, New York.
Sidor, C.A. and Hopson, J.A. (1998) Ghost lineages and 'mammalness': assessing the temporal pattern of character acquisition in the Synapsida. *Paleobiology* **24**, 254–273.

1.4 Mesozoic Events

1.4.1 Mesozoic Marine Revolution

P.H. KELLEY and T.A. HANSEN

Introduction

Two hundred years ago, the debate between catastrophists and uniformitarians dominated the nascent fields of geology and palaeontology. Although modern palaeontologists are at least nominally uniformitarians, many would reject Lyell's view of slow and steady change for a more catastrophic view of the history of life as a series of revolutions.

A marked restructuring of shallow marine benthic communities occurred during the middle and late Mesozoic, which has been called the Mesozoic marine revolution (Vermeij 1977). The changes included the intensification of grazing and the diversification of durophagous (shell-destroying) predators such as teleost fish, decapod crustaceans, and carnivorous gastropods. As a result of the intensified predation and grazing, bioturbation and the frequency of infaunal life modes increased, stalked crinoids and brachiopods disappeared from shallow-water habitats, and increases occurred in prey shell sturdiness and the frequency of shell repair (Vermeij 1977).

Mesozoic increases in predation and grazing

Most molluscivores appeared or developed durophagous habits (such as crushing, hammering, or peeling the growing edge of a shell) in the Mesozoic, particularly the Jurassic and Cretaceous (Vermeij 1977, 1987). Cephalopods developed crushing abilities in the Middle Triassic; other Triassic crushers were marine reptiles, such as placodonts and the ichthyosaur family Omphalosauridae, and possibly pycnodontiform and semionotiform fishes. The Jurassic marked the origin of such shell breakers as the Heterodontidae (sharks), Batoidea (rays), Stomatopoda (crustaceans), Palinuridae (spiny lobsters), Nephropidae (lobsters), Brachyura (crabs), and Aves (birds); most of these groups developed durophagy by the Cretaceous. Drilling gastropods (Naticidae and Muricidae) also diversified in the Cretaceous, as did other predatory gastropods (e.g. Buccinidae, Fasciolariidae, Melongenidae, Volutidae, Olividae). Other important Cretaceous durophagous predators were the mosasaurid lizards and ptychodontoid sharks. The radiation of durophagous predators has continued through the Cenozoic (Fig. 1.4.1.1). Grazing also accelerated during the later Mesozoic with the expansion of teleost fishes and sea urchins (Echinoidea; Vermeij 1977). Both groups scrape algae and epifaunal animals from hard substrates and are important determinants of community structure today, especially in reef environments.

Community response to the Mesozoic marine revolution

Various changes in benthic communities have been attributed to the increase in predation and grazing during the Mesozoic marine revolution. Communities of the Palaeozoic and early Mesozoic were dominated by

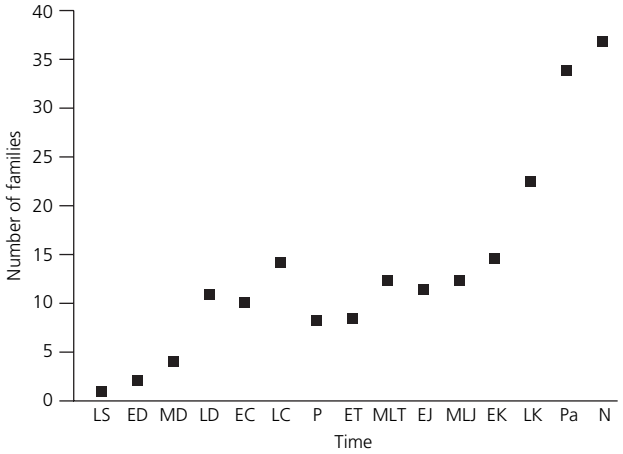

Fig. 1.4.1.1 Number of families of marine durophagous predators, including eurypterid and crustacean arthropods, cephalopod molluscs, and vertebrates. Abbreviations from left to right: LS, Late Silurian; ED, Early Devonian; MD, Middle Devonian; LD, Late Devonian; EC, Early Carboniferous; LC, Late Carboniferous; P, Permian; ET, Early Triassic; MLT, Middle–Late Triassic; EJ, Early Jurassic; MLJ, Middle–Late Jurassic; EK, Early Cretaceous; LK, Late Cretaceous; Pa, Palaeogene; N, Neogene. (After Vermeij 1987.)

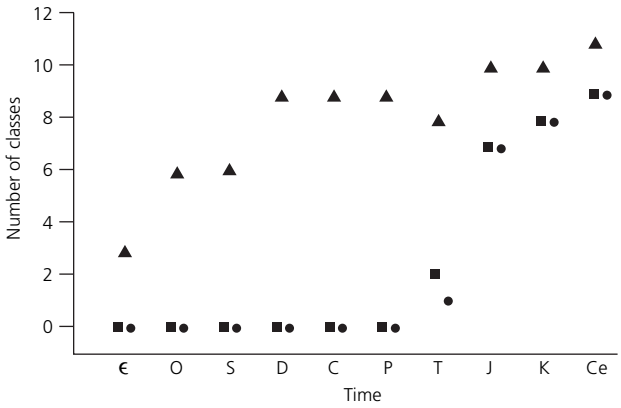

Fig. 1.4.1.2 Temporal changes in number of classes of bioturbating animals. Triangles, number of classes with bioturbating members; circles, number of classes with intensively bioturbating members (those that rework sediment at a rate of 10 cm^3/day); squares, number of classes with deeply bioturbating members (10 cm or more depth of bioturbation). (Modified from Vermeij 1987; data from Thayer 1983.)

epifaunal suspension-feeders, such as stalked crinoids, brachiopods, and epifaunal molluscs. In contrast, shallow-water soft-bottom communities of the later Mesozoic and Cenozoic were greatly impoverished in solitary epifaunal and semi-infaunal taxa. Both a retreat of epifaunal taxa to cryptic or deeper-water environments and infaunalization appear to have occurred.

Increased epifaunal predation and grazing apparently led to the displacement of stalked echinoderms and brachiopods to cryptic or deeper-water refugia and their replacement in shallow water by unstalked comatulid crinoids and byssally attached or cemented epifaunal bivalves (Vermeij 1977). The frequency of arm regeneration, and therefore predation, in modern Caribbean stalked crinoids is greater in shallower water, suggesting that increased predation pressure of the Mesozoic marine revolution caused the disappearance of stalked crinoids from shallow water and the consequent radiation of mobile comatulids. In addition, a statistically significant decrease of shallow-water dense ophiuroid populations ('brittlestar beds') occurred in the Early Cretaceous (Aronson 1989). The decline of these epifaunal suspension-feeding echinoderms is consistent with an intensification of predation and bioturbation during the Mesozoic marine revolution. The shift of such epifaunal taxa to deeper-water refugia reflects a general trend of onshore origination, followed by expansion (or retreat) to offshore habitats, which has been documented for several groups (Jablonski and Bottjer 1990).

A post-Palaeozoic increase in frequency of infaunal life modes among echinoids, gastropods, and especially bivalve molluscs has been noted (Stanley 1977). Although mantle fusion and the development of siphons permitted deeper and more rapid burrowing in the Bivalvia, widespread Mesozoic infaunalization has been attributed to increasing predation pressure (Stanley 1977). The role of predation is supported by the observation that extant epifaunal bivalves generally have traits that protect them against predation, such as thick shells, large size, commissural spines, ability to swim, or confinement to habitats in which predation is reduced. The replacement of epifaunal and semi-infaunal forms by infaunal taxa has been particularly marked since the Late Cretaceous (Vermeij 1977, 1987) or perhaps earlier. A significant increase in the percentage of shallow-burrowing to moderately deep-burrowing organisms, especially in shallow-shelf environments, began in the Middle Jurassic.

The trend of increasing infaunalization is consistent with a dramatic rise in bioturbation beginning in the Jurassic (Thayer 1983; Vermeij 1987) (Fig. 1.4.1.2), with drastic consequences for epifaunal attached and unattached organisms. Bioturbation may cause the burial of organisms that lie on the sediment surface; resuspended fine sediment may clog the filters of suspension-feeders. Increased bioturbation would thus have reinforced the role of predation and grazing in the Mesozoic elimination of epifaunal and semi-infaunal suspension-feeders from shallow-water habitats. Diversification of phytoplankton (coccolithophorids, dinoflagellates, and diatoms) in the late Mesozoic may also have been facilitated by the recycling of benthic nutrients, as bioturbators resuspended organic particles in the water column (Thayer 1983).

Changes in shell architecture also occurred during the Mesozoic marine revolution (Vermeij 1977, 1987). The incidence of mechanically sturdier, more highly armoured shells increased in the late Mesozoic, probably due to increased predation pressure. Among gastropods, shells with an umbilicus and planispiral or open coiling, which have little resistance to crushing predation, waned in importance after the early Mesozoic. For example, umbilicate species represented >25% of Palaeozoic and Triassic assemblages; after the Early Jurassic, such species never constituted more than 20% of warm-water faunas. Palaeozoic snails generally lacked nodes, spines, or ribs, whereas later Mesozoic taxa were characterized by sturdier, more highly sculptured shells resistant to breaking predation. In particular, the percentage of gastropod subfamilies with thickened or narrowed apertures increased steadily from zero in the Early Triassic to approximately 15% in the Late Cretaceous (and 20–30% in the Cenozoic). The ability to remodel the interior of the shell has allowed highly ornamented mesogastropods and neogastropods with apertures restricted by dentition to flourish since the Cretaceous. Elaboration of armour also occurred among cephalopods, bivalves, arthropods, and echinoderms, such as an increase in overlapping and crenulated shell margins among bivalves. However, locomotion may be more important than armour as an antipredatory defence for at least some members of these groups (Vermeij 1987).

A statistically significant increase in the frequency of repair scars, presumably caused by unsuccessful predation, is evident in the shells of Mesozoic gastropods from shallow-water soft-bottom assemblages (Vermeij 1987). In a Late Triassic assemblage, 18% of the abundant species had a frequency of shell repair >0.25; the corresponding value for the Late Cretaceous was 63%. Although an increase in sublethal attacks may have various causes (for instance, better-defended or older prey that accumulated a large number of scars), these data are also consistent with an increase in the abundance of shell-breaking predators during the middle Mesozoic.

Evolutionary dynamics, escalation, and the Mesozoic marine revolution

Although the rise in predation and the synchronous community restructuring and architectural changes of the Mesozoic marine revolution are generally accepted, the evolutionary dynamics of these changes are inadequately understood and their causes are debated. The Mesozoic decline of semi-infaunal, endobyssate taxa and their replacement by burrowing or epifaunal forms with antipredatory traits have been attributed to the differential extinction of species vulnerable to predation (Stanley 1977). This phenomenon has been referred to as 'species selection' or 'species sorting'. The Mesozoic marine revolution could represent the intensification of species selection or sorting by physical or geographical conditions of the Mesozoic that permitted synchronous changes in various groups (Vermeij 1977). For instance, biogeographical differentiation coupled with mild climate may have fostered the expansion of predators and well-armoured prey.

The Mesozoic marine revolution is one of several intervals during which both predation and the frequency of predation-resistant morphologies increased significantly. A similar radiation of durophagous predators and armoured prey occurred in the Middle to Late Devonian, termed the 'mid-Palaeozoic precursor to the Mesozoic marine revolution' (Signor and Brett 1984). Such results support a key role for biotic interactions, particularly predation, in evolution and form the basis for Vermeij's (1987) hypothesis of escalation. This hypothesis claims that, during the Phanerozoic, biological hazards (such as predation and competition) have increased and adaptations to these hazards have become better expressed. As a result, long-term trends have occurred in the morphology, behaviour, and distribution of organisms, such as those cited for the Mesozoic marine revolution. According to the hypothesis of escalation, these long-term trends have been driven by interactions with enemies (predators, competitors, and dangerous prey), which Vermeij views as the most important agents of natural selection. Escalation may involve coevolution, in which interacting species evolve reciprocally, if the species involved are mutual enemies (e.g. predators and dangerous prey). However, Vermeij argued that predators are more likely to respond evolutionarily to their own enemies (predators or competitors) than to antipredatory adaptation of benign prey. The extent to which such adaptation occurs within species or during speciation is unclear. Although intraspecific antipredatory adaptation has been reported in the bivalve prey of Miocene naticid gastropods (primarily increased shell thickness), Vermeij (1987) envisioned adaptation to enemies as occurring primarily during speciation and stated that differential diversification would lead to increased representation of species with antipredatory adaptations within a clade.

This view is consistent with the clade-level dynamics of aporrhaid gastropods, important prey taxa that diversified during the Mesozoic in two episodes, the Middle Jurassic and Late Cretaceous (Roy 1994). The initial radiation established two morphological groups, one with multidigitate, generally thin apertures, and the other with apparently sturdier, simpler apertures. The second radiation preferentially added species to the sturdier group with the apparently more predation-resistant architecture. Selection due to predation may have

created an origination bias in favour of the sturdier morphology; the sturdier taxa were also more widespread and thus more prone to speciation (Roy 1994).

Although interactions with enemies drive escalation, abiotic circumstances may produce episodes of escalation, such as the Mesozoic marine revolution. Vermeij argued that escalation of predator–prey or competitive relationships occurred episodically through the Phanerozoic and was fostered by intervals of climatic warming, transgression, and high productivity. Under such conditions, ecological limitations are relaxed and adaptive innovations can take hold. Episodes of massive submarine volcanism (such as during the later Mesozoic) raised water temperatures, caused transgression, and injected nutrients into the water column (Vermeij 1995). Productivity was enhanced by the warmer temperatures and higher nutrient levels. The warm temperatures and abundant and predictable resource supply allowed individual organisms to acquire more resources and permitted life modes requiring more energy (for instance, heavily calcified or mobile organisms with high metabolic rates). Such conditions also facilitated founder speciation (development of a new species by divergence of a small initial 'founder' population) by allowing the expansion of daughter populations. This scenario could account for the Mesozoic marine revolution, the early Palaeozoic development of predators, burrowers, and mineralized taxa, and possibly lesser episodes of diversification during the Phanerozoic (Vermeij 1995).

By the same argument, mass extinctions caused by cooling, drops in productivity, and/or regression should interrupt escalation (Vermeij 1987, 1995). Highly escalated species (those with antipredatory traits) should be particularly prone to extinction because of their higher metabolic requirements, whereas organisms with lower energy requirements are more likely to survive declines in productivity. According to the hypothesis of escalation, although mass extinctions apparently interrupted escalation, they did not undo the general trend of adaptation to enemies that pervaded the Phanerozoic (Vermeij 1995).

The occurrence of revolutions in the history of life, such as the Mesozoic marine revolution, is well documented. However, the broader but related concept of escalation remains controversial. Debate continues regarding the relative importance of biotic and abiotic factors in evolution, the reality of directional evolutionary trends, and the processes underlying the macroevolutionary patterns.

References

Aronson, R.B. (1989) A community-level test of the Mesozoic marine revolution theory. *Paleobiology* **15**, 20–25.

Jablonski, D. and Bottjer, D.J. (1990) Onshore–offshore trends in marine invertebrate evolution. In: R.M. Ross and W.D. Allmon, eds. *Causes of evolution: a paleontological perspective*, pp. 21–75. University of Chicago Press, Chicago.

Roy, K. (1994) Effects of the Mesozoic marine revolution on the taxonomic, morphologic, and biogeographic evolution of a group: aporrhaid gastropods during the Mesozoic. *Paleobiology* **20**, 274–296.

Signor, P. and Brett, C.E. (1984) The mid-Paleozoic precursor to the Mesozoic marine revolution. *Paleobiology* **10**, 229–245.

Stanley, S.M. (1977) Trends, rates, and patterns of evolution in the Bivalvia. In: A. Hallam, ed. *Patterns of evolution*, pp. 209–250. Elsevier, Amsterdam.

Thayer, C.W. (1983) Sediment-mediated biological disturbance and the evolution of marine benthos. In: M.J.S. Tevesz and P.L. McCall, eds. *Biotic interactions in recent and fossil benthic communities*, pp. 479–595. Plenum, New York.

Vermeij, G.J. (1977) The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology* **3**, 245–258.

Vermeij, G.J. (1987) *Evolution and escalation: an ecological history of life*. Princeton University Press, Princeton.

Vermeij, G.J. (1995) Economics, volcanoes, and Phanerozoic revolutions. *Paleobiology* **21**, 125–152.

1.4.2 Origin and Radiation of Angiosperms

E.M. FRIIS, K.R. PEDERSEN and P.R. CRANE

Introduction

Angiosperms (flowering plants) were the last major group of plants to appear in the fossil record; their first scattered occurrences are reported from the earliest Cretaceous. Angiosperms diversified and increased dramatically in abundance through the Cretaceous, and by the mid-Cretaceous they had attained ecological prominence in most parts of the world. The radiation of angiosperms in the Cretaceous led to profound changes in the composition of terrestrial plant communities, which included extinctions or marked declines in the diversity or abundance of many other groups of seed plants that had previously been important in Mesozoic vegetation, including Bennettitales, Cycadales, Ginkgoales, and, to a lesser extent, Gnetales. Conifers were also impacted by changes in Cretaceous ecosystems but several groups, for example Pinaceae, continued to diversify in parallel with the angiosperm radiation. In their rise to ecological dominance angiosperms exhibited extraordinary developmental and evolutionary plasticity, resulting in vegetative and reproductive

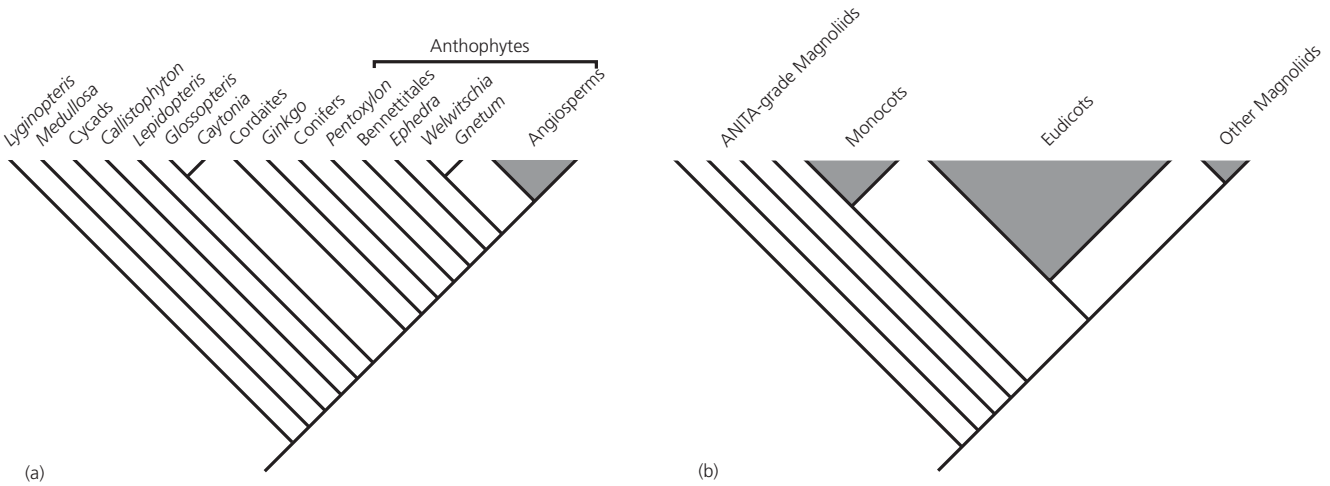

Fig. 1.4.2.1 Hypotheses of relationships among seed plants and angiosperms. (a) Cladogram showing one hypothesis of seed plant relationships where angiosperms are grouped with Gnetales, Bennettitales, and *Pentoxylon* in the anthophyte clade. (b) Cladogram showing relationships of angiosperms with monocotyledons and eudicotyledons nested in a paraphyletic magnoliid grade.

organs that are more diverse in structure than those of any other group of land plants.

Angiosperm origin

According to most traditional interpretations, as well as explicit phylogenetic analyses, angiosperms are a well-defined monophyletic group. Most morphology-based cladistic analyses including both extant and extinct taxa identify a monophyletic clade, often referred to as the anthophytes, comprising the angiosperms, Gnetales, Bennettitales, and *Pentoxylon* (Fig. 1.4.2.1a). Several molecular phylogenetic studies also place Gnetales as the closest living relatives to the angiosperms. The anthophyte concept has, however, been questioned by other analyses of which some resolve the conifers as most closely related to the Gnetales, and angiosperms as sister-group to all seed plants. Such discrepancies are most likely related to the relictual nature of living seed plants and the inherent difficulties of using molecular sequence data to resolve relationships among lineages that diverged long ago and have evolved independently since. Attempts to establish relationships among seed plants based on morphological data also confront substantial difficulties, particularly in establishing homologies among their vegetative and reproductive structures because of the incomplete knowledge currently available of the structural diversity in extinct taxa.

Although many theoretical models have been offered in attempting to reconcile the reproductive structures of angiosperms with those of other seed plants, many fundamental issues are still poorly understood, especially the derivation of the angiosperm carpel and the outer integument of the angiosperm ovule. Such uncertainties, combined with the substantial morphological gaps that separate angiosperms from other seed plants, greatly increase the difficulties of rooting the angiosperm tree, and establishing relationships among basal angiosperms. However, in general terms there is clear evidence that the subclass Magnoliidae comprises a paraphyletic basal grade of dicotyledons in which two major monophyletic groups, the monocotyledons and the eudicotyledons, are embedded (Fig. 1.4.2.1b). At the magnoliid grade there is also evidence that the extant taxa most likely to diverge at the very base of the angiosperm tree include Amborellaceae, Nymphaeaceae *sensu lato* (water lilies), Illiciales, Trimeniaceae, and Austrobaileyaceae (the so-called ANITA-grade; Fig. 1.4.2.1b).

Angiosperm characteristics

Angiosperms exhibit exceptional morphological diversity, particularly among their flowers, and this diversity is also manifested among plants at the magnoliid grade. Both large bisexual floral structures, consisting of numerous tepals, stamens, and carpels in a spiral arrangement (e.g. Magnoliaceae), and minute unisexual flowers consisting of just a single stamen or a single carpel (e.g. Chloranthaceae), occur among basal magnoliid angiosperms (Fig. 1.4.2.2). Unique defining characters that unite the angiosperms relate mainly to the reproductive system and include, most importantly, the presence of carpels enclosing the ovules, and stigmatic pollen germination that is often followed by growth of a pollen tube through the carpellary tissue. Most flowers

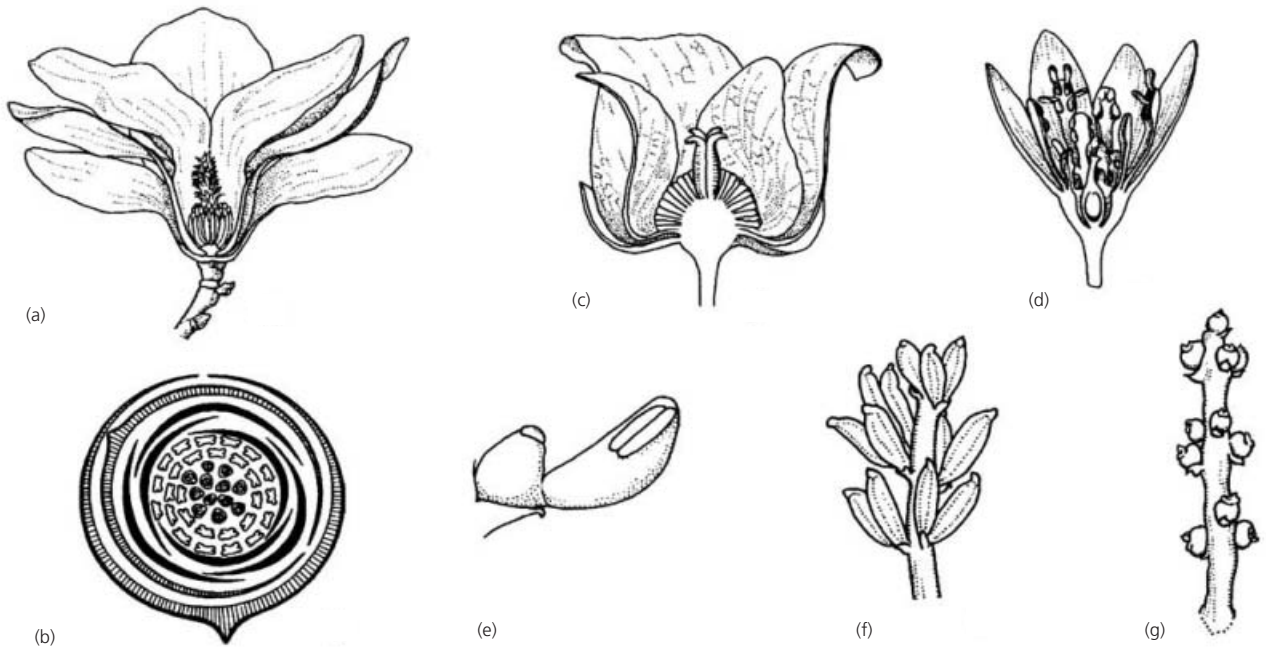

Fig. 1.4.2.2 Structural features of angiosperms (floral diversity in extant magnoliids). (a) Magnoliaceae. (b) Floral diagram of *Magnolia* flower. (c) Annonaceae. (d) Lauraceae. (e–g) Chloranthaceae; (e) bisexual flowers of *Sarcandra*; (f,g) unisexual flowers of *Ascarina*. (a,c–g, From Friis and Endress 1990; b, from Crane *et al.* 1995 with permission.)

are bisexual, with both carpels and stamens in the same flower, but unisexual flowers in which the stamens and carpels occur in separate flowers are also common in many widely scattered groups.

Angiosperm pollen grains also show much greater diversity in aperture configuration and wall structure than is seen in the pollen grains of other groups of seed plants. Angiosperm pollen grains are apparently distinguished from those of other seed plants by having a thin non-laminate inner layer of the pollen wall (endexine, Fig. 1.4.2.3f), while in other seed plants this layer is thick and laminate. Magnoliid angiosperms and monocotyledons typically have monoaperturate pollen grains with a single aperture (monocolpate, monoporate; Fig. 1.4.2.3d), a feature that they share with many non-angiospermous seed plants. In contrast, the pollen of eudicotyledons is distinguished from that of all other seed plants in having three or more apertures that are typically distributed in a radially symmetrical pattern around the equator (e.g. tricolpate, tricolporate, triporate; Fig. 1.4.2.3e,f). Among living seed plants, pollen with a reticulate–columellate pollen wall is restricted to the angiosperms. However, the interpretation of this feature as a defining characteristic of the group is complicated by the fact that it is not universally present in magnoliid angiosperms, and records of dispersed pollen from the Triassic (the Crinopolles-complex) indicate that reticulate and columellate pollen was perhaps also produced by non-angiospermous seed plants.

Angiosperm leaves typically have a broad leaf blade and a characteristic reticulate venation pattern formed by a hierarchical system of successively thinner veins and free ending veinlets (Fig. 1.4.2.3a). Reticulate venation also occurs in several other plant groups, but in these plants (except extant *Gnetum*) such venation is typically simpler and without free ending veinlets. Another vegetative feature characteristic of most angiosperms is the presence of vessels with scalariform or scalariform-derived pitting (Fig. 1.4.2.3b,c). The wood of most other seed plants lack vessels, as does that of a few living angiosperm taxa, but it is currently uncertain whether this reflects an ancestral or derived state in the context of angiosperms as a whole.

Timing of angiosperm origin and their first major radiation

The earliest angiosperm remains that can be recognized with certainty in the fossil record are dispersed, monoaperturate pollen grains with a reticulate–columellate outer pollen wall very similar to the pollen

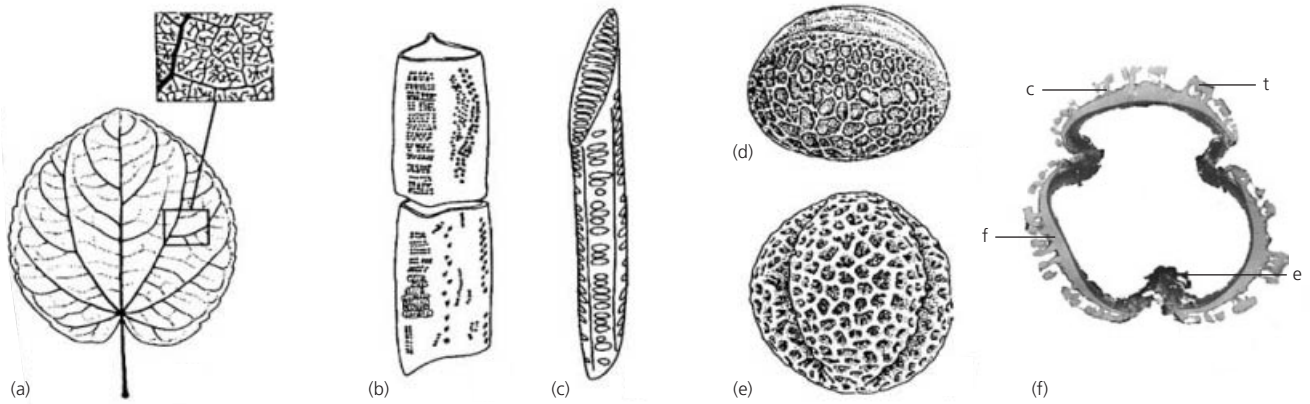

Fig. 1.4.2.3 Structural features of angiosperms (leaves, wood, pollen). (a) Leaf of *Cercidiphyllum* with hierarchical reticulate venation. (b,c) Vessel elements of angiosperm wood. (d,e) Angiosperm pollen with reticulate–columellate pollen wall; (d) monoaperturate grain of monocotyledon; (e) tricolpate grain of eudicotyledon. (f) Cross-section of tricolpate pollen grain showing pollen wall with tectum (t), columellae (c), foot layer (f), and granular endexine (e). (Line drawings by P. von Knorring.)

of living magnoliids and perhaps also certain monocotyledons. These pollen grains occur scattered in microfloras of Early Cretaceous age (Valanginian–Hauterivian). Angiosperm pollen is rare in these earliest microfloras, but has been reported over a wide geographical area extending from southern England to Italy, Morocco, and Israel, and perhaps to sites in Asia (Hughes 1994). By this time angiosperm pollen already shows considerable diversity in the form of the reticulum and tectum ornamentation (Hughes 1994). Currently there is no reliable evidence of angiosperms prior to the Cretaceous, and a reproductive structure with angiospermous features from northern China thought initially to extend the fossil record of angiosperms back to around the Jurassic–Cretaceous boundary now appears to be substantially younger (Barremian–Aptian).

The various phylogenetic models that have been put forward for angiosperm relationships all support the view that the lineage leading to angiosperms diverged prior to the Cretaceous. However, the firstmajor diversification and radiation of angiosperms clearly took place in the Early and mid Cretaceous. During this time interval the fossil record shows a marked increase in the diversity, structural complexity, and abundance of angiosperm pollen, leaves, and reproductive structures (Hickey and Doyle 1977; Crane *et al*. 1995; Friis *et al*. 1999).

Patterns of structural diversification — pollen and leaves

The earliest angiosperm pollen grains from Valanginian–Hauterivian microfloras all have a single aperture. The pollen wall typically has an outer reticulate layer supported by a layer of columellae (e.g. Hughes 1994). Among living plants this kind of pollen is known only from basal angiosperms at the magnoliid grade and monocotyledons. By the Barremian, monoaperturate pollen had diversified further, and the first appearance of pollen grains with three apertures (tricolpate) documents the establishment of eudicotyledonous angiosperms in Cretaceous vegetation (e.g. Hughes 1994). During the Aptian and Albian pollen of eudicotyledons diversified considerably, and by the end of the Cenomanian a variety of aperture types, including forms with three elongated apertures (tricolpate), three elongated apertures each with a central pore (tricolporate), and three pores (triporate) were widely distributed (Hickey and Doyle 1977).

The earliest scattered records of angiosperm leaves are from the Hauterivian–Barremian and Aptian. These leaf fossils are typically very small and simple with a disorganized venation pattern and often without a distinctly differentiated petiole. By the Albian, however, angiosperm leaves had attained considerable architectural diversity, typically with a regular and well-differentiated vein pattern and distinct petiole. Compound leaves also appear for the first time during the Albian (e.g. Hickey and Doyle 1977).

Patterns of structural diversification — floral structures

Numerous mesofossil floras with small well-preserved flowers, fruits, seeds, stamens, and other dispersed plant fragments have been discovered from Cretaceous strata in Europe, North America, Asia, and Antarctica (Knobloch and Mai 1986; Friis *et al*. 1994, 1999; Crane *et al*. 1995; Crepet 1996; Frumin and Friis 1998; Herendeen *et al*. 1999; Takahashi *et al*. 1999), mainly from Upper Cre-

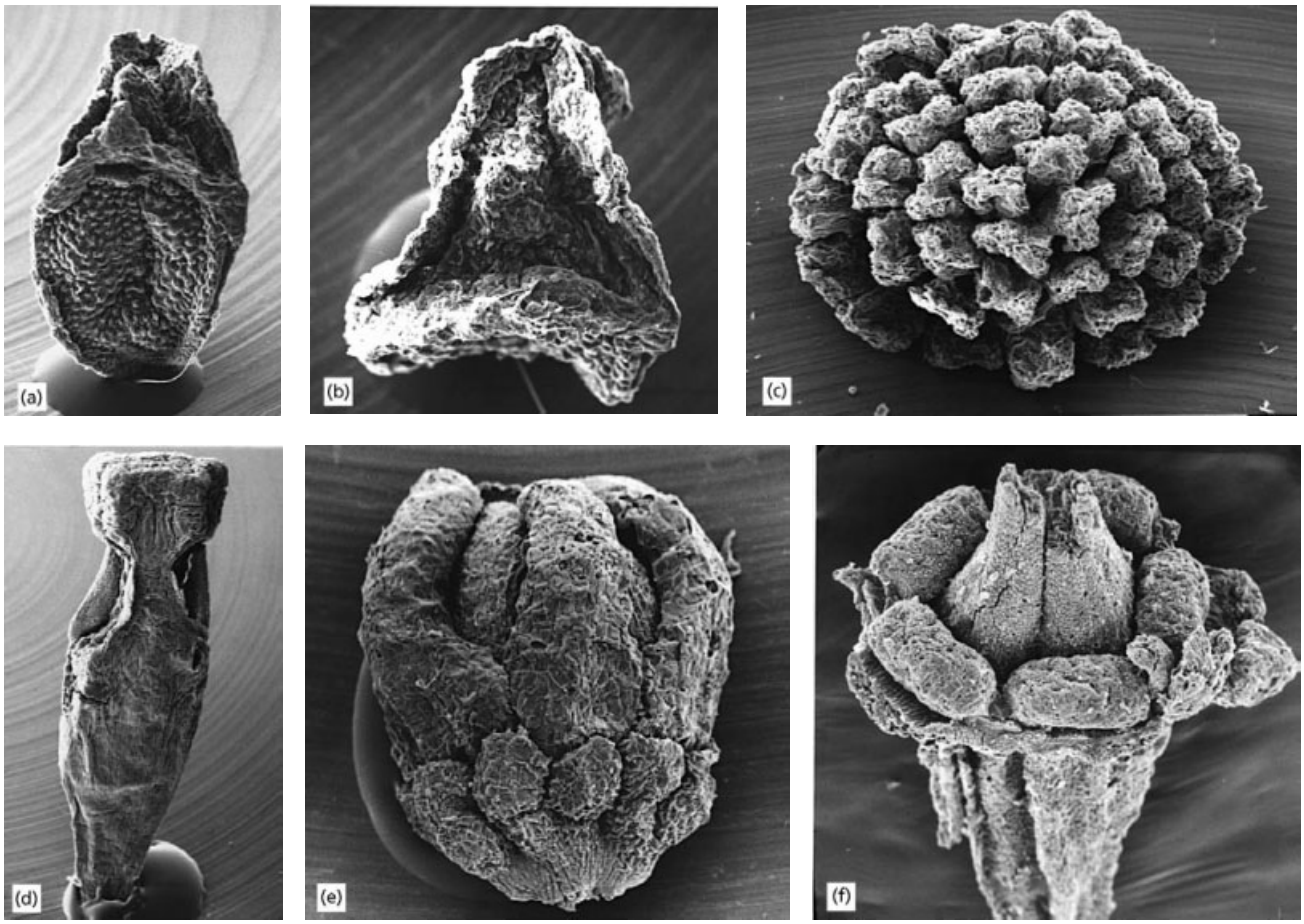

Fig. 1.4.2.4 Three-dimensionally preserved floral structures from the Cretaceous. (a,b) *Hedyosmum*-like female flower from the Barremian or Aptian of Portugal; (a) lateral view, ×54; (b) apical view, ×70. (c) *Hedyosmum*-like male inflorescence from the Barremian or Aptian of Portugal, ×65. (d) Isolated stamen from the Barremian or Aptian of Portugal with minute pollen sacs and a massive connective developed both between and apically to the pollen sacs, ×22. (e,f) Late Cretaceous flowers from southern Sweden; (e) *Scandianthus* showing calyx and corolla, ×70; (f) unnamed flower with distinct nectary, ×50. (All SEM-micrographs.)

taceous sediments, but several rich floras have also been discovered from Lower Cretaceous strata. The oldest abundant and well-preserved angiosperm mesofossils are in floras of Barremian or Aptian age from the Western Portuguese Basin (Friis *et al*. 1994, 1999). Many of these fossil angiosperm reproductive organs are charcoalified and retain their original three-dimensional shape and anatomical details (Fig. 1.4.2.4).

Studies of fossil flowers from the Cretaceous show that diverse kinds were established early in angiosperm evolution. With few exceptions, all floral structures, fruits, and seeds from the Cretaceous are very small, ranging from about 0.5 mm to 3–4 mm. Both unisexual and bisexual flowers are present in the earliest assemblages of fossil flowers. Early Cretaceous flowers are simple, typically with few floral organs, and either lack a floral envelope (perianth) or exhibit a perianth that is insignificant and poorly differentiated (Fig. 1.4.2.4a–c). Many stamens are characterized by having a poorly differentiated filament. Anthers often have small pollen sacs with valvate dehiscence and extensive sterile tissue between and above the pollen sacs (Fig. 1.4.2.4d). The ovary is formed from one or many carpels that are free from each other (apocarpous). Each carpel has a single or few ovules.

Several extant magnoliid taxa were established in the Early Cretaceous and some show a surprising lack of change in their floral organization. Most notably, flowers and dispersed pollen very similar to extant *Hedyosmum* (Chloranthaceae) occur abundantly in the Early Cretaceous (Fig. 1.4.2.4a–c) and appear to have remained unchanged for more than 100 million years after their first appearance in the Barremian–Aptian (Friis *et al*. 1999).

By the mid-Cretaceous the first angiosperm flowers with a well-differentiated floral envelope of sepals and petals, forming a calyx and a corolla respectively, are reported from fossil assemblages. The first records of flowers with an ovary of fused carpels and with nectaries also appear at the same time. The evolution of petals and the synorganization of carpels was a major step in the evolution of angiosperms and may have facilitated a further diversification among angiosperm subgroups through the Late Cretaceous and the early part of the Tertiary. To a large extent this Late Cretaceous–Tertiary diversification of angiosperms may have been closely linked to the evolution of more specialized pollination and dispersal syndromes involving coevolution with animal pollinators and dispersal agents. For example, many flowers from the Late Cretaceous have well-developed nectaries (Fig. 1.4.2.4f). Similarly, there is a clear increase in the maximum size of angiosperm fruits and seeds in the Early Tertiary.

By the end of the Cretaceous and Early Tertiary, many extant genera and families of angiosperms were already differentiated. However, major diversification in many of the most diverse groups of living angiosperms evidently continued through the Tertiary up to the present. Among these late radiating angiosperm groups are the grasses, and grass-dominated ecosystems were established in many parts of the world during the Miocene and Pliocene. The differentiation of other modern ecosystems, such as the tropical rain forests or boreal conifer forests, was apparently also mainly a Tertiary event.

References

Crane, P.R., Friis, E.M. and Pedersen, K.R. (1995) The origin and early diversification of angiosperms. *Nature* **374**, 27–33.

Crepet, W.L. (1996) Timing in the evolution of derived floral characters: Upper Cretaceous (Turonian) taxa with tricolpate and tricolpate derived pollen. *Review of Palaeobotany and Palynology* **90**, 339–359.

Friis, E.M. and Endress, P.K. (1990) Origin and evolution of angiosperm flowers. *Advances in Botanical Research* **17**, 99–162.

Friis, E.M., Pedersen, K.R. and Crane, P.R. (1994) Angiosperm floral structures from the Early Cretaceous of Portugal. *Plant Systematics and Evolution* **8** (Suppl.), 31–49.

Friis, E.M., Pedersen, K.R. and Crane, P.R. (1999) Early angiosperm diversification: the diversity of pollen associated with angiosperm reproductive structures in Early Cretaceous floras. *Annals of the Missouri Botanical Garden* **86**, 259–296.

Frumin, S. and Friis, E.M. (1998) Magnoliid reproductive organs from the Cenomanian-Turonian of north-western Kazakhstan. *Plant Systematics and Evolution* **216**, 265–288.

Herendeen, P.S., Magallón-Puebla, S., Lupia, R., Crane, P.R. and Kobylinska, J. (1999) A preliminary conspectus of the Allon flora from the Late Cretaceous (late Santonian) of central Georgia, USA. *Annals of the Missouri Botanical Garden* **86**, 407–471.

Hickey, L.J. and Doyle, J.A. (1977) Early Cretaceous fossil evidence for angiosperm evolution. *Botanical Review* **43**, 2–104.

Hughes, N.F. (1994) *The enigma of angiosperm origins*. Cambridge University Press, Cambridge.

Knobloch, E. and Mai, D.H. (1986) Monographie der Früchte und Samen in der Kreide Von Mitteleuropa. *Rozpravy ústredního ústavu geologickénho, Praha* **47**, 1–219.

Takahashi, M., Crane, P.R. and Ando, H. (1999) Fossil flowers and associated plant fossils from the Kamikitaba locality (Ashizawa Formation, Futuba Group, lower Coniacian, Upper Cretaceous) of Northeast Japan. *Journal of Plant Research* **112**, 187–206.

1.4.3 Rise of Birds

L.M. CHIAPPE

Introduction

'. . . if the whole hind quarters, from the ilium to the toes, of a half-hatched chicken could be suddenly enlarged, ossified, and fossilized as they are, they would furnish us with the last step of the transition between Birds and Reptiles; for there would be nothing in their characters to prevent us referring them to the Dinosauria.'
(T.H. Huxley 1869)

The origin of birds—Aves, the clade that originated from the common ancestor of *Archaeopteryx* and living birds—has been a matter of scientific debate and scrutiny throughout the history of taxonomy and evolutionary biology. In the eighteenth century, birds were placed immediately ahead of flying fishes in the 'chain of being'. With the establishment of evolutionary theories, more explicit hypotheses of relationships were formulated. During the nineteenth and twentieth centuries, birds were considered to be related to a variety of extinct and extant lineages of reptiles, including turtles, lizards, crocodylomorphs, pterosaurs, theropod and ornithischian dinosaurs, and a range of basal archosauromorphs (Witmer 1991) (Fig. 1.4.3.1).

Since J. Ostrom revitalized T.H. Huxley's hypothesis of the theropod origin of birds almost 30 years ago (Padian and Chiappe 1998), a large quantity of fossil documentation supporting a dinosaurian ancestry has been accumulated. Today, despite disagreement regarding the specific taxon phylogenetically closest to birds (e.g. dromaeosaurids, troodontids, oviraptorids), several lines of evidence converge to sustain the origin of birds

from maniraptoriform theropods (i.e. the common ancestor of *Ornithomimus* and Aves plus all its descendants; Fig. 1.4.3.1), no longer leaving any reasonable doubt that extant birds are short-tailed, feathered, maniraptoriform theropods (see also Section 4.1.13). (For other, less substantiated hypotheses of bird origins, see Witmer 1991 and Padian and Chiappe 1998.)

Evidence for the maniraptoriform origin of birds

The most visible evidence that birds are phylogenetically nested within maniraptoriform theropods is based on comparisons of their osteology, behaviour, oology, and integument with that of a variety of non-avian maniraptoriforms.

Osteology

A multitude of derived osteological characters are shared by all, or some, non-avian maniraptoriform theropods and birds. Comparisons between these taxa are greatly assisted by the many newly discovered basal birds (Padian and Chiappe 1998), which possess a skeletal morphology only slightly modified from the ancestral maniraptoriform condition. Some of these derived characters are the presence of rostral, dorsal, and caudal tympanic recesses (air spaces connected to the ear region), ventral processes on cervicothoracic vertebrae, ventral segments of thoracic ribs, forelimbs that are more than half the length of hindlimbs, a semilunate carpal bone allowing swivel-like movements of the wrist, clavicles fused into a wishbone, a pubic peduncle of the ilium longer than the ischiadic peduncle (these peduncles form the front and rear borders of the hip-socket), a vertically to caudoventrally orientated pubis ending in a boot-like expansion that projects only caudally, an ischium two-thirds or less the length of the pubis, and a femur with a feeble fourth trochanter (the attachment of the caudofemoralis longus muscle).

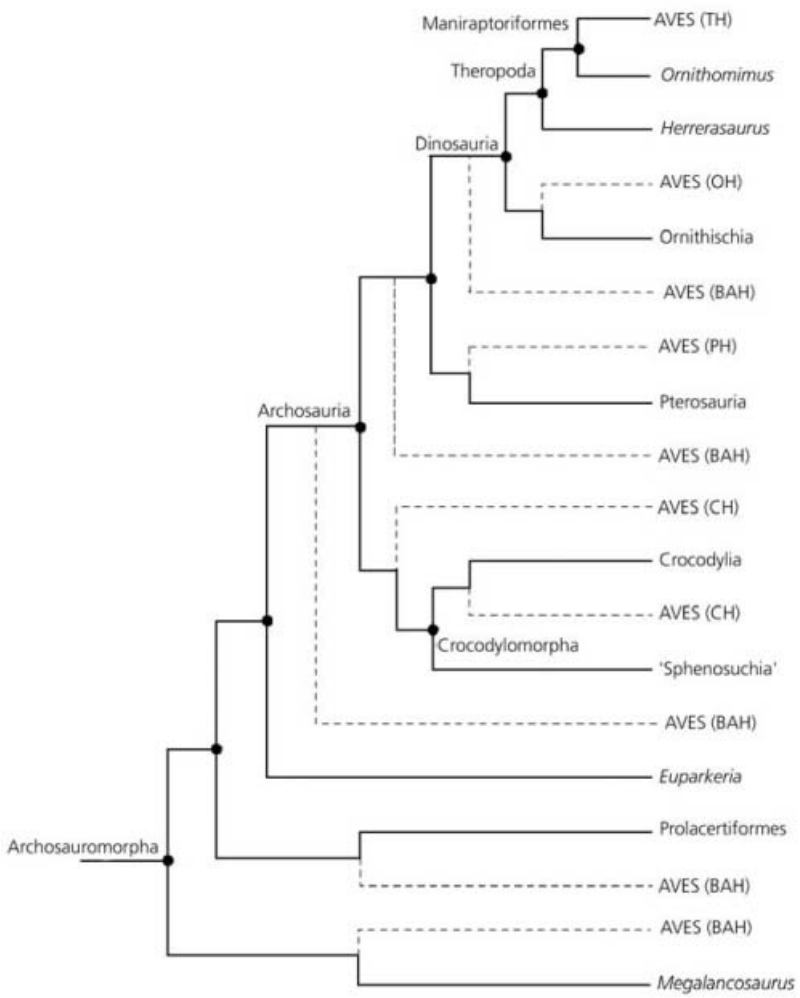

Fig. 1.4.3.1 Cladogram (derived from several cladistic analyses) depicting the phylogenetic relationships between various groups of archosauromorph reptiles and the diversity of hypotheses of bird origins advocated in the last three decades. BAH, array of often vague and somewhat different hypotheses that can be called the 'basal archosauromorph hypotheses'. CH, the initial 'crocodylomorph hypothesis' supported a close relationship between crocodylomorphs and birds; its current version places birds closer to extant crocodiles than to 'sphenosuchians'. OH, the 'ornithischian hypothesis'. PH, the 'pterosaur hypothesis'. TH, the 'theropod hypothesis' or, more properly, the 'maniraptoriform hypothesis'.

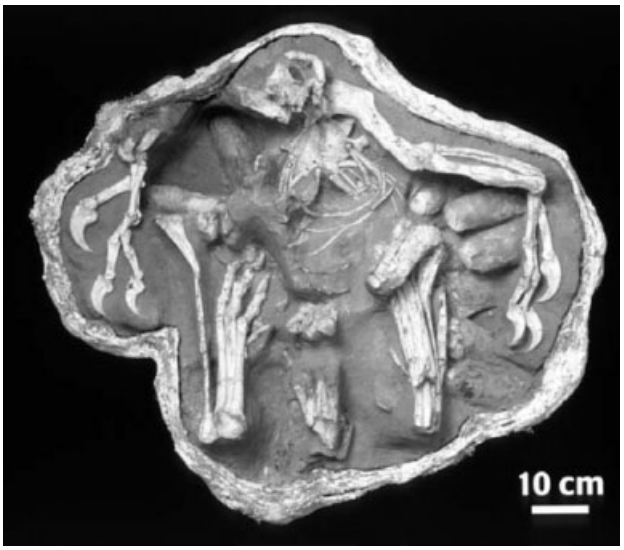

Fig. 1.4.3.2 Oviraptorid discovered on top of a clutch of oviraptorid eggs by the 1993 American Museum of Natural History–Mongolian Academy of Sciences expedition to Ukhaa Tolgod (Gobi Desert) (Clark *et al.* 1999). The behaviour inferred for this specimen, that of resting on top of presumably its own clutch of eggs, is a typical avian feature. (The specimen is IGM 100/979, Mongolian Institute of Geology, Ulan Bataar.)

Behaviour

Evidence of the behaviour of extinct organisms is rarely preserved in the fossil record. A handful of extraordinary discoveries, however, have shed light on the nesting conduct of certain non-avian maniraptoriforms. Several skeletons of Late Cretaceous oviraptorids from the Gobi Desert have been discovered on top of their clutches of eggs (Fig. 1.4.3.2). An oviraptorid embryo inside an egg of comparable morphology to those in these clutches strongly supports the idea that these specimens were brooding their own nest (Clark *et al.* 1999). A similar discovery of a Late Cretaceous troodontid skeleton from Montana in an identical brooding position suggests that, regardless of its specific function (e.g. protection, incubation), the typical avian nesting behaviour (i.e. adults sitting on top of their nests) was widespread among non-avian maniraptoriforms.

Oology

The general morphology and microstructure of calcified eggs is specific to certain groups of extant and extinct reptiles (Mikhailov 1997). Until recently, the precise characteristics of the eggshell microstructure of non-avian theropods remained elusive due to the absence of diagnostic embryonic material. The discovery of the Gobi oviraptorid embryo provided the first definitive evidence of a non-avian theropod egg (Clark *et al.* 1999). Since then, other non-avian maniraptoriform embryos have been found. Comparative studies between the eggshell microstructure of these eggs and those of extant birds have revealed features singular to the maniraptoriform type of eggshell, which define the ornithoid basic type (Mikhailov 1997). This basic type is unique in having shell units with at least two distinctly separated microstructural zones. The innermost zone is formed by a calcite crystalline structure that radiates from an organic core; the external zone has a scaly microstructural arrangement. In birds this external zone may grade into, or be completely separated from, a third, outermost zone. No other reptilian egg is known to have these microstructural characteristics (Mikhailov 1997).

Integument

Feathers have always been the quintessential bird feature. Unquestionable feathers are known in two maniraptoriforms, *Protarchaeopteryx* and *Caudipteryx*, from the Early Cretaceous of China (Ji *et al.* 1998). Down-like feathers are preserved covering portions of the several known specimens of these taxa. A fan-shaped cluster of pennaceous feathers (with a shaft and vanes) is attached to the distal part of the tail and symmetrically vaned feathers anchor to the distal portion of the forelimbs of *Caudipteryx*.

Initial cladistic analyses (Ji *et al.* 1998) placed *Caudipteryx* as the sister-taxon of birds, and *Protarchaeopteryx* in an unresolved trichotomy with velociraptorine dromaeosaurids and the clade formed by *Caudipteryx* and birds. Subsequent studies nested *Caudipteryx* within oviraptorosaurs. The fact that these two maniraptoriforms exhibit the primitive condition for several avian synapomorphies as well as for other synapomorphies diagnosing less inclusive clades of birds, makes it improbable that future cladistic analyses would nest them within birds.

Criticisms of the maniraptoriform hypothesis of bird origins

The 'temporal paradox'

Some critics of the maniraptoriform origin of birds (e.g. Feduccia 1996) have taken issue with the chronological gap between the oldest bird, the Late Jurassic *Archaeopteryx*, and the Cretaceous non-avian maniraptoriforms typically used in discussions of bird origins (e.g. *Deinonychus*, *Velociraptor*, *Oviraptor*). This criticism has become known as the 'temporal paradox' since it highlights the supposed inconsistency of arguing that birds evolved from creatures that lived several million years after their own origin. The 'temporal paradox', however, is meaningless because none of these Cretaceous dinosaurs has ever been regarded as the direct

ancestor of birds (Padian and Chiappe 1998). The maniraptoriform hypothesis postulates the existence of a most recent common ancestor of these Cretaceous dinosaurs and *Archaeopteryx* that obviously existed before the differentiation of the oldest of these taxa, *Archaeopteryx*. Advocates of the 'temporal paradox' often overlook the fact that Late Jurassic maniraptoriforms have been known for several decades (Padian and Chiappe 1998). Remains of putative maniraptoriforms (e.g. ornithomimids, therizinosaurids) were subsequently discovered in the Late Triassic of the USA and the Early Jurassic of China, suggesting that maniraptoriform theropods may have differentiated long before the known history of birds.

Embryology of the avian hand

Opponents of the dinosaurian origin of birds (e.g. Feduccia 1996; Burke and Feduccia 1997) often highlight the conflict between the identity of the avian wing digits, as suggested by embryological studies, and that indicated by the palaeontological evidence. Embryological investigations of extant birds have identified the digits of the hand as II, III, and IV of the pentadactyl limb and extrapolate this conclusion to include all birds. In contrast, the fossil record of non-avian theropods documents a reduction of digits IV and V throughout their evolution; these two digits disappeared prior to the differentiation of the maniraptoriforms (Padian and Chiappe 1998). Furthermore, the morphology, proportions, and phalangeal formula of the manual digits of certain maniraptoriforms (e.g. *Velociraptor*, *Deinonychus*) are remarkably similar to those of *Archaeopteryx*, indicating that the digits of the hand of *Archaeopteryx* are likely homologous to digits I, II, and III of the pentadactyl hand.

Despite the extrapolations made by critics of the maniraptoriform hypothesis, the real problem resides in whether the homology of the digits of *Archaeopteryx* is the same as that of modern birds, a difficult problem to address since the hand of modern birds is highly transformed and embryological data are unavailable for *Archaeopteryx*. Thus, even if the identity of the wing digits of modern birds is that indicated by the embryological data, the hand of *Archaeopteryx* may still have been formed by the same developmental trajectory of non-avian maniraptoriforms. The shift in this developmental trajectory may well have evolved after the differentiation of the lineage leading to *Archaeopteryx*. Consequently, the embryological research on the hand of extant birds (e.g. Burke and Feduccia 1997) is irrelevant to the understanding of bird origins; it bears only on their later evolution. Common usage notwithstanding, the extrapolation of the embryological pattern observed in modern birds to all birds (including *Archaeopteryx*) is unwarranted.

Lung structure and ventilation

Based on interpretations of soft structures alleged to be indicators of visceral compartmentalization and the morphology of the pubis, non-avian theropods have been reconstructed with a crocodile-like, hepatic-piston mechanism for lung ventilation (Ruben *et al.* 1997), in which lung inflation is a consequence of the liver being pulled by a series of muscles attached to the pubis. These authors argued that their interpretation of the lung structure and ventilation of non-avian theropods posited serious caveats to the theropod origin of birds. They contend that the transition from the crocodile-like pulmonary system of non-avian theropods to the flow-through lung system of birds would have required the evolution of an opening in the alleged partition between the thoracic and abdominal cavities of non-avian theropods, a diaphragmatic hernia (Ruben *et al.* 1997). Such a hernia would have compromised the efficiency of the pulmonary system of the transitional forms (Ruben *et al.* 1997).

The available osteological evidence of non-avian theropods, especially of non-avian maniraptoriforms, shows that several of the skeletal correlates of the avian flow-through lung were already present among those dinosaurs. Pneumatic foramina for the entrance of air-sac diverticula are widespread among the vertebrae of non-avian theropods. Intracostal articulations delimiting ossified costal and ventral ribs are known for dromaeosaurids and oviraptorids (Clark *et al.* 1999), and these and other maniraptoriforms have relatively large ossified sternal plates. The morphology of the ribs and sternum of these theropods suggests that the coordinated costal and sternal movements that ventilate the lungs of extant birds may have already been present in their maniraptoriform ancestors.

Non-avian theropods may have had a crocodile-like diaphragm dividing their visceral cavity (Ruben *et al.* 1997), but the presence in these dinosaurs of skeletal features correlated to the avian system of lung structure and ventilation is undeniable. Even if we were to reconstruct the lung ventilation system of non-avian theropods in a crocodile-like fashion, the alleged implausibility of this system evolving into the ventilatory mechanism of birds remains to be demonstrated.

Conclusion

In 1960, the origin of birds was thought to be largely a matter of deduction, with 'no fossil evidence of the stages through which the remarkable change from reptile to bird was achieved' (Swinton 1960). Since then, features that for decades highlighted the uniqueness of birds, from furculae and swivel-like wrists, to feathers and nesting behaviour, have been discovered among

non-avian maniraptoriform theropods. Specifics notwithstanding, the origin of birds from maniraptoriform dinosaurs is indisputable. Criticisms levelled by detractors are misleading. The main transformations from non-avian maniraptoriforms to modern birds are beautifully preserved in the fossil record.

References

Burke, A.C. and Feduccia, A. (1997) Developmental patterns and the identification of homologies in the avian hand. *Science* **278**, 666–668.

Clark, J.M., Norell, M.A. and Chiappe, L.M. (1999) An oviraptorid skeleton from the Late Cretaceous of Ukhaa Tolgod, Mongolia, preserved in an avian-like brooding position over an oviraptorid nest. *American Museum Novitates* **3265**, 1–36.

Feduccia, A. (1996) *The origin and evolution of birds*. Yale University, New Haven.

Ji Q., Currie, P., Norell, M.A. and Ji S.-A. (1998) Two feathered dinosaurs from northeastern China. *Nature* **393**, 753–761.

Mikhailov, K.E. (1997) Fossil and recent eggshell in amniotic vertebrates: fine structure, comparative morphology and classification. *Special Papers in Palaeontology* **56**, 1–80.

Padian, K. and Chiappe, L.M. (1998) The origin and early evolution of birds. *Biological Reviews* **73**, 1–42.

Ruben, J.A., Jones, T.D., Geist, N.R. and Hillenius, W.J. (1997) Lung structure and ventilation in theropod dinosaurs and early birds. *Science* **278**, 1267–1270.

Swinton, W.E. (1960) The origin of birds. In: A.J. Marshall, ed. *Biology and comparative physiology of birds*, Vol. 1, pp. 1–14. Academic Press, New York.

Witmer, L.M. (1991) Perspectives on avian origins. In: H.-P. Schultze and L. Trueb, eds. *Origins of the higher groups of tetrapods: controversy and consensus*, pp. 427–466. Cornell University Press, Ithaca, New York.

1.5 Cenozoic Events

1.5.1 Evolution of Modern Grasslands and Grazers

T.E. CERLING

Introduction

Grass-dominated ecosystems, and those where grasses make up a significant fraction of the flora, are globally widespread. Tropical savannahs make up more than half the land area at low latitudes, and grass-dominated ecosystems are abundant in parts of North America and central Asia. Modern grasses use two different photosynthetic pathways, the more ancient 'C_3 pathway' and the more recent 'C_4 pathway', where 'C_3' and 'C_4' refer to the number of carbon atoms in the first product during CO_2 assimilation. The C_4 pathway includes a CO_2 enrichment mechanism which is absent in the C_3 pathway. The study of carbon isotopes, which distinguish between the C_3 and C_4 photosynthetic pathways, has demonstrated that the rise of 'modern grasslands' (i.e. grasslands where C_4 grasses are significant) is much later than the rise of grasslands in general.

The traditional view of the rise of grasses and grasslands is closely tied to the observation that equids and other mammals developed hypsodont (high-crowned) teeth in the Early Miocene (Simpson 1951) in North America. This view is supported by observations that fossilized grass and grass pollen appear in the Miocene in some abundance and become more common from the Miocene to the present. This increase in hypsodonty in mammals occurred in the Oligocene in South America and therefore it is thought that grasses were significant somewhat earlier in South America and possibly Africa (Jacobs *et al.* 1999). Unfortunately, grasses are most abundant in settings that are not conducive to the preservation of fossil plants in the geological record; they are common in oxidizing and well-drained environments where they tend to be destroyed after burial. Stable isotopes offer a new view of the development of grasses and grasslands, especially those grasses that are found today in tropical to warm temperate environments.

Grasses belong to the family Poaceae and all are monocotyledons. Grasses, particularly C_4 grasses, have several properties that make them very different from C_3 dicotyledons: (1) they tend to have lower nitrogen contents which make them intrinsically less nutritious than dicotyledons; (2) C_4 and C_3 grasses rarely have secondary toxins, which are found in many C_3 dicotyle-

dons; (3) protein in C_4 plants is 'protected' in the bundle sheath cells, making them harder to digest than protein in the thinner mesophyll cells of C_3 plants (Ehleringer *et al.* 1997); and (4) grasses have higher silica contents than dicotyledons, making them more abrasive. This last property provided the supposed link between the increase in hypsodonty in mammals in the Early Miocene and the development of savannah and grassland ecosystems. Thus, the traditional view is that hypsodonty evolved so that mammals could take advantage of the new food source available, i.e. grasses (see Simpson 1951; MacFadden 1992).

The rise of modern C_4 grasslands

Stable isotopes apparently provide a test for the hypothesis that the increase in hypsodonty in the Late Miocene is linked with the spread of grasses. This is because C_3 plants (including grasses) have $\delta^{13}C$ values of about –26‰ while C_4 plants (which are mostly grasses) have $\delta^{13}C$ values of about –12‰. In the modern world, C_4 grasses are the dominant grass at latitudes less than about 40°. Fossil teeth record the proportion of C_3/C_4 biomass in diets, and palaeosol carbonates record the proportion of C_3/C_4 biomass in ecosystems. Thus, carbon isotopes should record when C_4 grasses became abundant. In several ways, dietary evidence is preferable to palaeosol evidence for studying global ecosystem changes: (1) the identification of fossils is less problematic than of palaeosols; (2) museums around the world have rich collections that can be studied; and (3) the selective nature of dietary preferences enhances the distinction between C_3 and C_4 biomass.

Unfortunately, the story is complicated by the presence of both C_3 and C_4 grasses. Most C_4 plants are grasses, and they are the dominant grass at low to intermediate latitudes; however, C_3 grasses are found in regions with cool growing seasons, such as are found at high latitudes, high altitudes, or in Mediterranean (i.e. winter-rain) climates. Therefore the isotope record documents only the increase in C_4 grasses, as opposed to the increase in grasses. C_3 grasses have the same $\delta^{13}C$ values as C_4 dicotyledons.

The carbon isotope record of equids from North America shows an abrupt increase in ^{13}C starting about 7 Ma (Fig. 1.5.1.1), corresponding to the time when equids began to have a significant component of C_4 biomass in their diets (Cerling *et al.* 1997). The isotope enrichment between diet and bioapatite is about 14‰, so that $\delta^{13}C$ values <–8‰ indicate a diet dominated by C_3 biomass while $\delta^{13}C$ values >0‰ indicate a diet dominated by C_4 biomass. This diet change occurred millions of years after hypsodonty appeared and equids became diversified (Fig. 1.5.1.1). In North America not all equids changed from a C_3 diet to C_4 grasses at this time: in more northern latitudes and along the Pacific Coast the advent of C_4 grasses in the diet was much delayed or absent altogether. Only in the southern USA and in Mexico did some equids become sole C_4 consumers. At the end of the Miocene (≈7–5 Ma), in southern Asia (Pakistan) and in Africa (Kenya) equids changed from being predominantly (>90%) C_3 consumers to predominantly (>90%) C_4 grazers (Cerling *et al.* 1997). Equids were not present in South America at this time, but other hypsodont mammals show an expansion of C_4 biomass at the end of the Miocene. Therefore, the carbon isotope record from

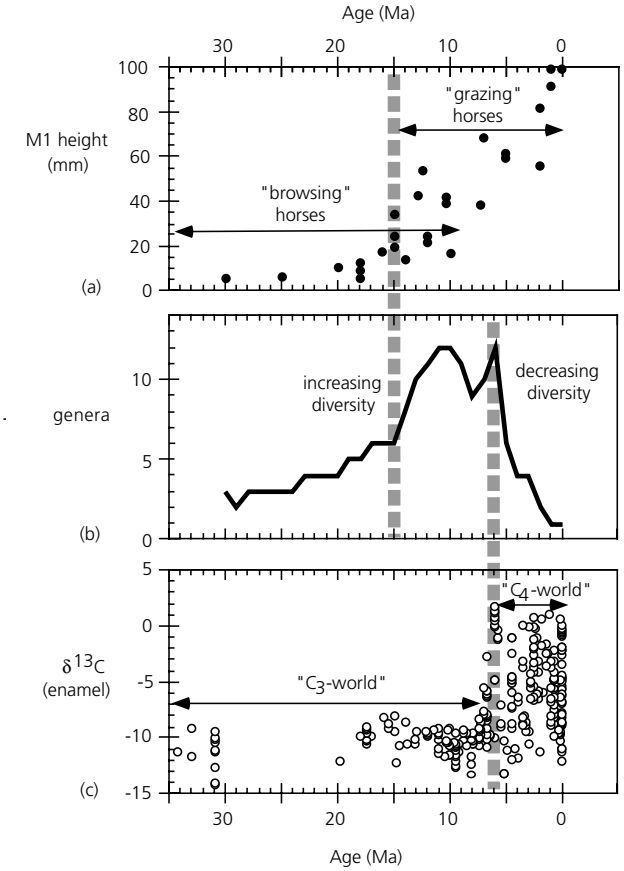

Fig. 1.5.1.1 (a) Development of increasing hypsodonty in North American equids; M1, first upper molar tooth. (b) Increasing diversity of equids between 20 and 15 Ma; the simultaneous increase in hypsodonty and diversity has been generally taken to indicate the expansion of grasses in the Early Miocene in North America. (c) North American equids underwent a significant dietary change beginning about 7 Ma when they began to eat C_4 grasses; this coincides with a significant decrease in the diversity of equids. Dashed lines show that increasing hypsodonty and diversity are correlated in time, and that the rise of C_4 grasses correlates with the decrease in equid diversity. (a, Modified from Wang *et al.* 1994; b, data from MacFadden 1992.)

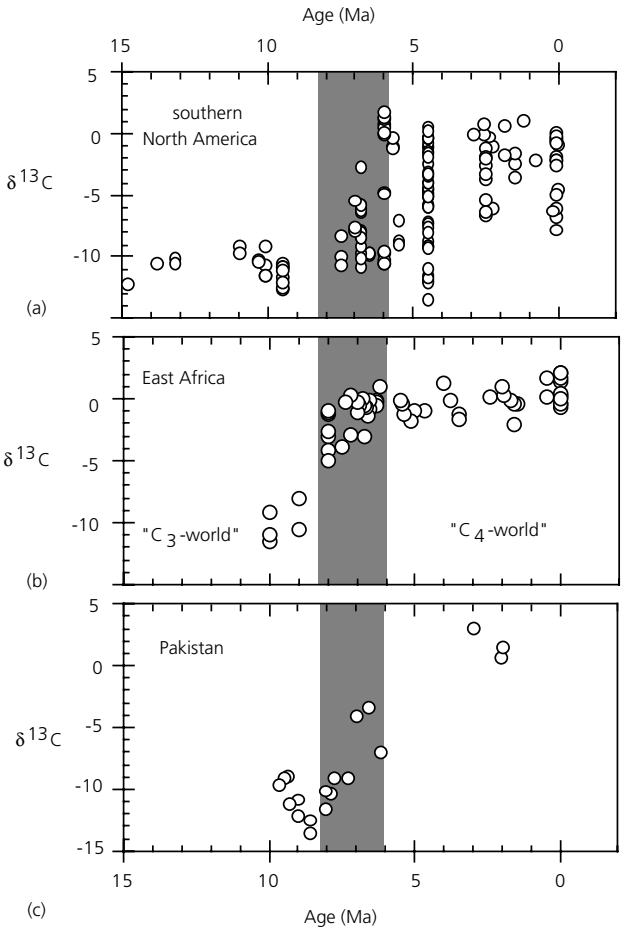

Fig. 1.5.1.2 $\delta^{13}C$ values for equids in: (a) southern North America (Florida, Texas, Arizona, Mexico); (b) Africa; (c) Pakistan. All show an abrupt increase in $\delta^{13}C$ in the Late Miocene, indicating that in all regions C_4 biomass became an available food resource. The details of the relative timing of the C_4 biomass expansion is under study. Equids immigrated from North America to the Old World at about 10.5 Ma. These first immigrants to the Old World had C_3 diets as shown. (Data from Cerling *et al*. 1997.)

four continents indicates that C_4 grasses underwent significant expansion at the end of the Miocene—a time of significant faunal change on each of these continents, including Europe. The carbon isotope record from Europe, however, does not show significant C_4 biomass at any time. The post-Miocene C_3 signal for equid diets in Europe could be due either to browsing of C_3 dicotyledons or to a diet of C_3 grass. The isotope record cannot distinguish between grazers and browsers when C_3 grasses are the dominant grass.

The $\delta^{13}C$ isotope record clearly shows a global increase in C_4 biomass at the end of the Miocene (Fig. 1.5.1.2). Major faunal turnover of mammals occurs on most continents at this time. The inception of modern grasslands, which are dominated by C_4 grasses at low to intermediate latitudes, began in the Late Miocene and developed fully in the Early to Middle Pliocene. It is still reasonable to assume that grasses developed in the Early Miocene, but it is now clear that modern grasslands developed much later. The grassland and savannah ecosystems of today (i.e. dominated by C_4 grasses) are of Late Miocene origin.

The conditions that favour C_4 photosynthesis are high temperatures and low concentrations of atmospheric carbon dioxide; these conditions promote photorespiration in C_3 plants. C_4 monocotyledons have a higher quantum yield than C_3 monocotyledons or dicotyledons above about 20–25°C for atmospheric CO_2 levels of 350 ppm (Ehleringer *et al*. 1997). The crossover temperature, where C_4 monocotyledons have a higher quantum yield than C_3 monocotyledons and dicotyledons, occurs at higher temperatures at higher CO_2 levels; the crossover at 500 ppm CO_2 is about 28–33°C. Because growing temperatures rarely exceed ≈ 35°C anywhere on Earth, 500 ppm CO_2 may represent the upper limit for ecosystems where C_4 plants would be more competitive than C_3 plants.

References

Cerling, T.E., Harris, J.M., MacFadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V. and Ehleringer, J.R. (1997) Global vegetation change through the Miocene/Pliocene boundary. *Nature* **389**, 153–158.

Ehleringer, J.R., Cerling, T.E. and Helliker, B.R. (1997) C_4 photosynthesis, atmospheric CO_2, and climate. *Oecologia* **112**, 285–299.

Jacobs, B.F., Kingston, J.D. and Jacobs, L.L. (1999) The origin of grass-dominated ecosystems. *Annals of Missouri Botanical Garden* **86**, 590–643.

MacFadden, B.J. (1992) *Fossil horses: systematics, paleobiology, and evolution of the family Equidae*. Cambridge University Press, New York.

Simpson, G.G. (1951) *Horses: the story of the horse family in the modern world and through sixty million years history*. Oxford University Press, New York.

Wang, Y., Cerling, T.E. and MacFadden, B.J. (1994) Fossil horses and carbon isotopes: new evidence for Cenozoic dietary, habitat, and ecosystem changes in North America. *Palaeogeography, Palaeoclimatology, Palaeoecology* **107**, 269–279.

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1.5.2 Radiation of Tertiary Mammals

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Introduction

The Tertiary Period was the time when mammals radiated into the great variety of body sizes and morphological diversities seen today. However, the Tertiary represents only about one-third of the total time of mammalian existence (see Section 1.3.10). The first mammals appeared in the latest Triassic, but during the Mesozoic they were all of small body size (the largest was about the size of a house cat) and mostly of generalist insectivorous/omnivorous adaptations. Although it seems unlikely that Mesozoic mammals were in direct competition with dinosaurs, not until the latter's demise at the end of the Cretaceous did mammals diversify into a broader variety of ecomorphological types.

The Tertiary is traditionally divided into the earlier Palaeogene and the later Neogene (Fig. 1.5.2.1). However, the mammalian faunas better reflect the division between the 'hot house world' of the earliest Tertiary (Paleocene and Early Eocene), a continuation of the warm global temperatures and ice-free world of the Mesozoic, and the 'ice house world' of the later Tertiary to Recent. The end of the Early Eocene represents the point of highest mean annual temperatures in higher latitudes, which subsequently plummeted to levels resembling those of the present day (with some amelioration during the Miocene). The Antarctic ice cap first appeared in the later Eocene, and the Arctic ice cap was established by the Pliocene. The generic diversity of mammals tracks the palaeotemperature curve, with an initial peak in the Early/Middle Eocene (and subsequent Late Eocene extinctions), and a second peak in the Middle Miocene (followed by Late Miocene extinctions) (Fig. 1.5.2.1). The well-known Late Pleistocene mammal extinction was less extensive than these earlier events and primarily affected larger mammals.

The evolutionary history of many mammalian lineages is from small, relatively unspecialized forms in the early Tertiary to the larger, more specialized Recent forms. This is exemplified by the famous textbook '*Eohippus*' to *Equus* story of horse evolution, where the morphological changes are usually interpreted as progressive moves to a fitter, 'better adapted' type of animal. However, the history of Tertiary mammals is better understood in the context of changing global climates and environments, brought about by shifting continents and tectonic events (see Janis 1993; Bernor *et al.* 1996). In this view, the early horse *Hyracotherium* (='*Eohippus*') is interpreted as well adapted to the global tropical-like forests of the Early Eocene. The replacement of early horses by later forms of larger body size, better adapted for eating grasses and running on the plains, reflects the cooling and drying of higher latitude environments, with temperate woodlands and grasslands replacing the tropical forests. Had North America (the site of horse evolution) been connected to South America during the early Tertiary, then *Hyracotherium*-like horses might have been able to migrate with their original habitat toward the equator and survive today, in a fashion similar to the mouse deer (tragulids) of the Old World tropics.

The role of continental drift and the isolation of mammalian faunas

Much of Tertiary (and modern) mammalian diversity is related to the isolation of different founder groups of mammals on different continents, and subsequent convergent evolution of similar ecomorphological types. The most obvious example today is the separate nature of the Australian marsupials, with their own iteration of various adaptive types such as 'moles', 'anteaters', and 'wolves', etc. Later Tertiary dispersals have muted or obliterated many differences in mammalian faunas between different continental blocks—only Australia has retained its relative isolation. The fauna of South America has some unique elements today, such as edentates (sloths, anteaters, and armadillos) and opossum-like marsupials, but around half the modern genera are derived from Northern Hemisphere immigrants that arrived when the Isthmus of Panama formed around 2.5 Ma. A large diversity of original endemic forms, most notably a great variety of ungulates (hoofed mammals) and large marsupial carnivores (borhyaenids), are now extinct (although their demise was not directly related to the arrival of the Pliocene immigrants).

The break-up of Pangaea began in the middle Mesozoic, and some workers have suggested that the global distribution of mammalian stocks was related to a vicariance event with the Cretaceous isolation of continents (Hedges *et al.* 1996). However, the more traditional view, and that supported by the fossil record, is that the Tertiary distribution of mammals is largely explained by dispersal events. Considering again the isolated nature of the Australian mammal fauna, the unique presence of monotremes (egg-laying mammals such as the platypus and echidna) may reflect vicariance. (Note, however, that the discovery of a platypus in the Paleocene of southern South America hints at an originally broader, Gondwanan distribution.) However, the Australian marsupials clearly arrived by dispersal from the Americas. The earliest marsupials are known from North America, and fossils from Antarctica support the hypothesis that they dispersed via a southern route prior to the complete isolation of Australia. The oldest Tertiary

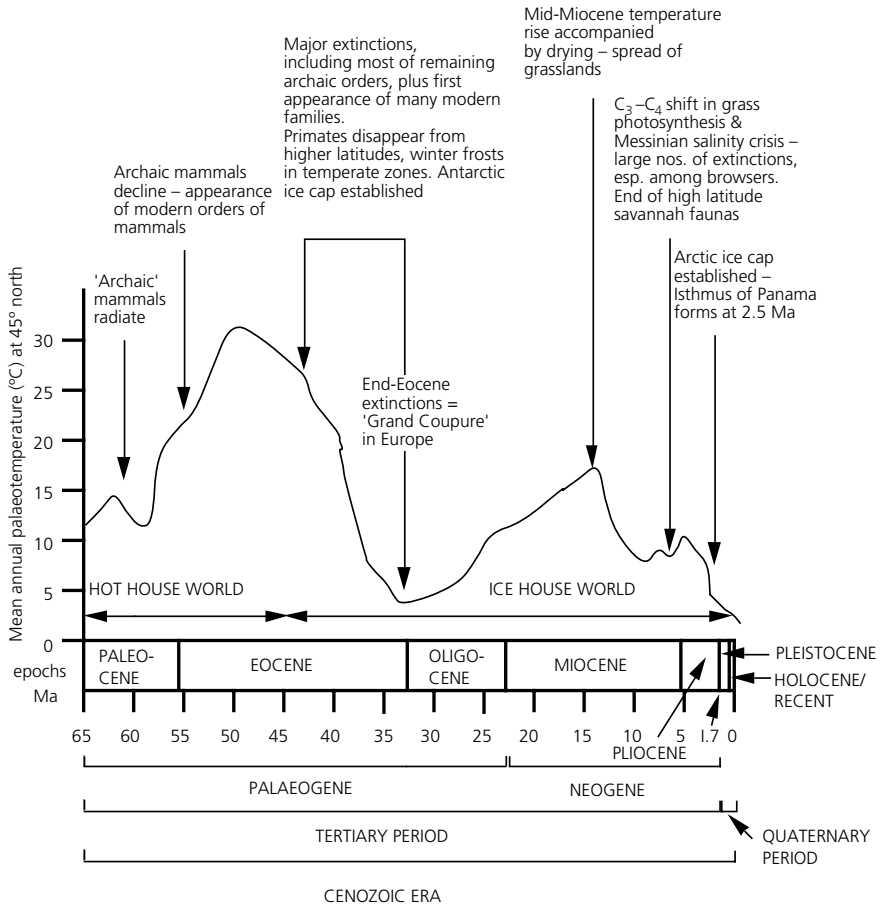
Mid-Miocene temperature rise accompanied by drying – spread of grasslands
Major extinctions, including most of remaining archaic orders, plus first appearance of many modern families. Primates disappear from higher latitudes, winter frosts in temperate zones. Antarctic ice cap established
C_3–C_4 shift in grass photosynthesis & Messinian salinity crisis – large nos. of extinctions, esp. among browsers. End of high latitude savannah faunas
Archaic mammals decline – appearance of modern orders of mammals
Arctic ice cap established – Isthmus of Panama forms at 2.5 Ma
'Archaic' mammals radiate
End-Eocene extinctions = 'Grand Coupure' in Europe
Mean annual palaeotemperature (°C) at 45° north
30
25
20
15
10
5
0
HOT HOUSE WORLD
ICE HOUSE WORLD
epochs
Ma
PALEO-CENE
EOCENE
OLIGO-CENE
MIOCENE
PLIOCENE
PLEISTOCENE
HOLOCENE/ RECENT
65 60 55 50 45 40 35 30 25 20 15 10 5 1.7 0
PALAEOGENE
NEOGENE
TERTIARY PERIOD
QUATERNARY PERIOD
CENOZOIC ERA

Fig. 1.5.2.1 Important events in Tertiary mammal evolution, related to palaeoclimatic curves for the Northern Hemisphere. (Palaeotemperature data from Burchardt 1978.)

fauna of Australia (Early Eocene) contains not only marsupials but also a single tooth of a placental, with its tantalizing suggestion that both marsupials and placentals initially dispersed to Australia but that only the former prevailed.

The island of Madagascar today provides a wonderful example of evolution in isolation: while many of its organisms represent a vicariance event since its Mesozoic split from Africa, its unique mammalian fauna (including lemurs, civet-like carnivores, and tenrec insectivores) was clearly derived from dispersal events, either from the African mainland or from Asia. Africa also contains a number of old endemic mammals, such as elephants, hyraxes, and aardvarks. Their original isolation may represent early vicariance, but most of the modern African fauna was obtained by dispersal from Eurasia, especially when Africa docked with Asia during the Oligocene.

Tertiary radiations and changing global climates

The mammals of the Paleocene largely represent 'archaic' groups. The majority of extant orders, most notably Primates, Cetacea (whales), and the ungulate orders Artiodactyla (pigs, camels, antelope) and Perissodactyla (horses, rhinos) date from the earliest Eocene. Rodents and bats are known from the Late Paleocene. Much information on the early Tertiary comes from the Northern Hemisphere. In the global tropical-like forests of the Paleocene the arboreal mammals were the squirrel-like plesiadapiform 'pro-primates', opossum-like marsupials, and the rodent-like multituberculates (an extinct subclass of mammals, holdovers from the Mesozoic). Terrestrial herbivores were primitive ungulates ('condylarths'), and forms of uncertain taxonomic affiliation (such as taeniodonts and pantodonts). The teeth of most of these animals suggest an omnivorous diet. Folivorous (leaf-eating) mammals were not apparent until the Eocene, perhaps reflecting a more deciduous type of vegetation associated with a more seasonal climate. Early carnivores were either the mesonychid 'condylarths' (which included the ancestors of whales) or the creodonts. These predators were all heavily built ambushers. The modern order Carnivora also appeared in the earliest Tertiary, but the earliest members ('miacoids') were small generalists and did not assume the role of larger predators until the Late Eocene.

Although many more modern groups of mammals first appeared in the Late Paleocene or Early Eocene, the more archaic groups did not immediately become extinct; their demise seems more related to the declining temperatures and changing vegetation of the later Eocene, which also affected some of the early modern types such as the higher-latitude lemuriform primates. The major extinctions occurred in the late Middle Eocene in North America, and close to the Eocene/Oligocene boundary in Europe (the 'Grand Coupure'). Dispersal of Asian mammals to Europe, following the drying up of the Turgai Straits at the end of the Eocene, may also be related to the magnitude of this extinction event. Evidence for Late Eocene mammalian extinctions elsewhere in the world is equivocal. A Grand Coupure event appears to have occurred in Asia (Meng and McKenna 1998), but critical faunas are missing in southern continents. Despite the more southerly Eocene position of Australia, a Grand Coupure type of replacement of an early Tertiary tropical-like fauna with one more adapted to cooler, drier conditions (e.g. containing kangaroos) is not apparent until the Pliocene.

Oligocene faunas represent a rather depauperate world without much diversification. By this time South America had received its faunal elements of rodents and monkeys, probably arriving from Africa by chance rafting. The major vegetation in the higher latitudes was now temperate woodland, perhaps with some arid patches. Grasslands were unknown, as were Arctic types of vegetation such as tundra and taiga. The major types of modern mammals are represented by extinct families belonging to modern orders, such as amphicyonids ('bear dogs') and nimravids ('false sabre-tooths') among the carnivores. By the Miocene, the higher-latitude temperatures started to rise again, to reach a Neogene maximum in the middle of the epoch. By the late Early Miocene, most Oligocene lineages were extinct, or on the wane, and the fauna began to take on a more modern aspect, dominated by members of extant families.

By the Middle Miocene, grasslands were spreading across the higher latitudes, and with them appeared mammals with adaptations for grazing, such as hypsodont (high-crowned) cheek teeth. Late Miocene faunas in Argentina and on the Great Plains of North America approached the ecomorphological diversity of mammals on the East African savannahs today, although of different taxonomic affiliations. For example, in North America a diversity of horses, camels, and pronghorns stood in for the African diversity of antelope. It is a popular notion that these new, longer-legged herbivores evolved in association with pack-hunting carnivores, but the fossil evidence shows that pursuit-type long-legged carnivores did not appear until the Pliocene. The longer legs of these Miocene ungulates were probably an adaptation for traversing a broader foraging territory in the drier, less productive environments (Janis and Wilhelm 1993).

This later Miocene spread of grasslands was traditionally attributed to Neogene mountain uplift (e.g. Rockies, Andes, Himalayas), which resulted in a rainshadow drying effect. However, the floral changes may have been driven by declining levels of atmospheric carbon dioxide, with a major shift in the carbon cycle biochemistry of grasses (from C_3 to C_4) at around 7 Ma in the latest Miocene (e.g. Cerling *et al.* 1998) (see Section 1.5.1). Drying was certainly an environmental factor, as evidenced by the latest Miocene desiccation of the Mediterranean sea (the Messinian salinity crisis). Whatever the reasons, major Late Miocene extinctions affected the high latitude mammal faunas as the savannah-like treed grassland habitat gave way to prairie (see Janis *et al.* 2000). Grazers were affected as well as browsers; in North America a diversity of over a dozen sympatric genera of grazing horses in the Late Miocene was reduced to a single genus in the Late Pliocene.

By the start of the Pliocene, an Arctic ice sheet was established, and tundra and taiga vegetation were present. A slight warming in the Early Pliocene was followed by a profound cooling at 2.5 Ma, resulting from changes in ocean currents following the establishment of the Isthmus of Panama. South American faunas were changed forever with the immigration of northern forms, while some southern forms (e.g. armadillos, opossums, monkeys) entered North America. Other late Tertiary dispersals resulted in present-day distributions of mammals: the dispersal from North America to the Old World of dogs, derived horses, and camels; the dispersal from the Old World to North America of deer, microtine rodents, and (in the Pleistocene) bovids (e.g. bison); and the dispersal of rodents from Asia to Australia (an event that had surprisingly little effect on the native fauna). In East Africa, the tropical forests gave way to savannahs at this time, resulting in the diversification of modern groups such as the bovids (antelope) and the emergence of humans (see Section 1.5.5).

Understanding Tertiary environmental changes provides the key to understanding mammalian evolution. Differences between early Tertiary and present-day mammals are largely the result of a change from equable, globally tropical conditions to a cooler, drier, and more climatically zoned world. Eocene-like mammals remain in the restricted equatorial forests (e.g. lemurs and mouse deer), but grazers have diversified in the grasslands (e.g. modern horses and antelope), and temperate woodland mammals in the higher latitudes (e.g. deer and bears), while some extreme specialists have evolved adaptations to environmental conditions unique to the past few million years (e.g. polar bears in the Arctic and camels in the desert).

References

Bernor, R., Fahlbush, V. and Mittleman, H.-W., eds. (1996) *The evolution of Western Eurasian Neogene mammal faunas*. Columbia University Press, New York.

Burchardt, B. (1978) Oxygen isotope palaeotemperatures from the Tertiary period in the North Sea area. *Nature* **275**, 121–123.

Cerling, T.E., Ehleringer, J.R. and Harris, J.M. (1998) Carbon dioxide starvation, the development of C_4 ecosystems, and mammalian evolution. *Philosophical Transactions of the Royal Society of London B* **353**, 159–171.

Hedges, S.B., Parker, P.H., Sibley, C.G. and Kumar, S. (1996) Continental breakup and the ordinal diversification of birds and mammals. *Nature* **381**, 226–229.

Janis, C.M. (1993) Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Annual Review of Ecology and Systematics* **24**, 467–500.

Janis, C.M. and Wilhelm, P.B. (1993) Were there pursuit predators in the Tertiary? Dances with wolf avatars. *Journal of Mammalian Evolution* **1**, 103–126.

Janis, C.M., Damuth, J. and Theodor, J.M. (2000) Miocene ungulates and terrestrial primary productivity: where have all the browsers gone? *Proceedings of the National Academy of Sciences, USA* **97**, 7899–7904.

Meng, J. and McKenna, M.C. (1998) Faunal turnovers of Palaeogene mammals from the Mongolian Plateau. *Nature* **394**, 364–367.

1.5.3 Rise of Modern Land Plants and Vegetation

M.E. COLLINSON

Introduction

Plants are primary producers—photoautotrophs which manufacture metabolites via photosynthesis—and are therefore at the base of the food chain for most life (except chemoautotrophic microbes). Vegetation forms the framework and provides the niches for other organisms (both above and below ground level). Plants and vegetation are therefore critical for understanding the history of life on land and the origin and evolution of modern land biomes.

The earliest modern biome?

Amongst modern land biomes tropical rain forests are familiar because of issues involving their fate due to human impact. However, asking palaeobiologists 'When was the earliest tropical rain forest?' may yield answers ranging from the Upper Carboniferous to only a few thousand years before present. None of these answers is incorrect, but all require further explanation.

In the Upper Carboniferous, peat (ultimately coal)-forming and clastic swamp forests existed in equatorial latitudes, so these indeed were equatorial wet areas with trees (i.e. 'tropical rain forest'). These forests included tall trees of various canopy heights, with understorey, scrambling plants, climbers, and epiphytes like modern tropical rain forests (see Section 1.3.8). However, their diversity was very low compared to modern tropical rain forests and the dominant plants (e.g. arborescent lycophytes and other spore bearers, seed ferns) and animals were utterly different in their taxonomy and functional biology from those that dominate the modern tropical rain forest biome (Krings and Kerp 1999). At the other extreme, the suggestion of a very recent origin assumes that tropical rain forest biotas, identical to those of the present day, could not have originated until after the influence of the last glaciation on global climates. A more appropriate approach is to evaluate the origin of modern biomes from the time when the dominant groups of organisms today first became dominant in the past.

The rise to dominance of modern land life

With the exception of moss-lichen tundra, and boreal conifer forests (taiga), most of the land surface today is dominated by flowering plants, even in lakes and in the seagrass banks of shallow seas. Numerous specializations of the reproductive (closed carpels, receptive stigma, double fertilization, faithful pollination, fruit variety and dispersal strategies) and vegetative (broadly laminate leaves, vessels in woods) organization of flowering plants distinguish their functional biology from that of other plants (Collinson 2000). Therefore, the rise of modern land vegetation must be considered to have begun after the rise of flowering plants. The means by which the fossil record of flowering plants is interpreted in terms of ancient vegetation is explained elsewhere (Collinson 2000).

Flowering plants appeared and diversified rapidly during the mid to Late Cretaceous. They rose to dominance in the rock record by about 90 Ma and in the Late Cretaceous a number of modern flowering plant families can already be recognized (Wing and Boucher 1998; Lupia *et al.* 2000). However, major modernization of flowering plants only occurred with their second radiation during the latest Cretaceous and early Cenozoic (Palaeogene) (Collinson 1990, 2000). This radiation resulted in numerous trees, shrubs, and lianas belonging to a high diversity of modern flowering plant families and genera (many represented by reconstructed whole plant fossils). Important plants included the para-

phyletic magnoliid dicotyledons (magnolias, bays, custard apples, water lilies), the dicotyledon subclasses Hamamelidae (planes, birches, walnuts, beeches, elms, casuarinas) and Rosidae (legumes, dogwoods, maples, grape vines), and monocotyledons (some herbaceous) of the subclasses Alismatidae (many lacustrine and pond plants such as pond weeds), Arecidae (palms and aroids), and Zingiberidae (gingers and bananas) (Collinson 2000).

Until the terminal Cretaceous extinctions the dominant groups of land vertebrates were the dinosaurs and pterosaurs. The mammals and birds did not rise to dominance until the early Cenozoic (Palaeogene), and many insect groups, which interact with plants in modern vegetation, were also unimportant until the Palaeogene (Friis *et al.* 1987; Collinson and Hooker 1991; Benton 1993). Therefore, the rise of modern land biomes is essentially an early Cenozoic phenomenon.

Tropical forests

The Early Eocene London Clay Flora of southern England, and similar floras elsewhere, can be reconstructed as Eocene tropical to paratropical forest. (Paratropical is similar to tropical but with fewer canopy layers.) The floras are diverse (up to 350 species) and include a wide range of flowering plant trees, shrubs, and lianas, the nearest living relatives of many of which are important in, or exclusive to, modern tropical rain forests (e.g. members of the families Arecaceae [palms], Anacardiaceae [cashew nut family], Anonaceae [custard apples], Burseraceae [sources of myrrh and frankincense], mastixioid Cornaceae [mastic trees], Dilleniaceae [Dillenias], Icacinaceae [Icacina vines], Lauraceae [cinnamon and bay trees], Menispermaceae [moonseed vines], Sabiaceae [*Sabia* and *Meliosma* trees and shrubs], and Vitaceae [grape vines, virginia creeper]). Physiognomic signatures from woods and leaves support the reconstruction of megathermal or warm mesothermal, broadleaved, evergreen vegetation, with tropical to subtropical climate regimes (Collinson 2000). (Mean annual temperatures (MAT) greater than 20°C sustain megathermal vegetation; MAT is 13–20°C and below 13°C for mesothermal and microthermal vegetation, respectively.) This vegetation was probably emplaced following increased humidity after the Cretaceous/Tertiary transition. Although there are flowering plant trees from at least three subclasses of dicotyledons in the Late Cretaceous, these are only known from low palaeolatitudes and their wood physiognomy does not indicate a rain forest setting. At the Eocene thermal maximum, the first extensive warm interval since their emplacement, the Eocene tropical forests spread up to palaeolatitudes ranging between 55 and 65° N and S. Their subsequent range restriction, both to lower latitudes and limited geographical areas (e.g. South-East Asia) was a consequence mainly of climatic change, especially global cooling, initiated in the Late Eocene and enhanced by terminal Eocene events (Collinson 2000).

The framework of Eocene tropical forests was formed by a high diversity of flowering plants, including trees, shrubs, and lianas, and their animal life was dominated by mammals and insects, as in modern tropical rain forests. Near living relatives of many of the Eocene biotic elements, and animal–plant interactions also documented in the Eocene, occur in tropical rain forests today and some are unique to this biome (Collinson 1990, 2000; Collinson and Hooker 1991). However, there are also differences. In European Eocene tropical forests the very limited occurrence of Dipterocarpaceae (a single macrofossil) is a major difference from modern South-East Asian rain forests (Collinson 2000). Furthermore, flowering plant epiphytes, so common in modern rain forests, lack a Palaeogene macrofossil record (Collinson 2000). Dipterocarp-dominated tropical rain forests like those of the present day in South-East Asia are considered to have developed during the Miocene (Morley 2000).

Mangroves

A *Nypa*-dominated mangrove (*Nypa* is a palm with a creeping stem) with subordinate occurrences of the mangrove family Rhizophoraceae (e.g. *Ceriops*) is reconstructed as the Early and Middle Eocene coastal vegetation of the former English, French, and Belgian North Sea coastlines (Fig. 1.5.3.1a,b) (Collinson 2000). Modern *Nypa*-dominated mangroves are common in South-East Asia (Collinson 2000). The *Nypa*-dominated mangrove may have been in place at low latitudes in the Late Cretaceous but during the Eocene thermal maximum it had expanded to palaeolatitudes approximately 55–65° N and S (Collinson 2000). A fossil record based largely on pollen grains indicates Middle Eocene occurrences for other mangroves (such as *Sonneratia*, *Brownlowia*, and *Oncosperma*) (Morley 2000).

Deciduous forests

The *in situ* tree stumps and litter layers of the Eocene fossil forests of Axel Heiberg Island (Canadian Arctic Archipelago, palaeolatitude 75–80°N) represent an excellent example of the Paleocene and Eocene vegetation of the high northern palaeolatitudes which has been termed polar broadleaved deciduous forest. These polar deciduous forests were of relatively low diversity and dominated by wind-pollinated, dry fruited, deciduous trees of the flowering plant families Betulaceae (birch trees), Cercidiphyllaceae/Trochoden-

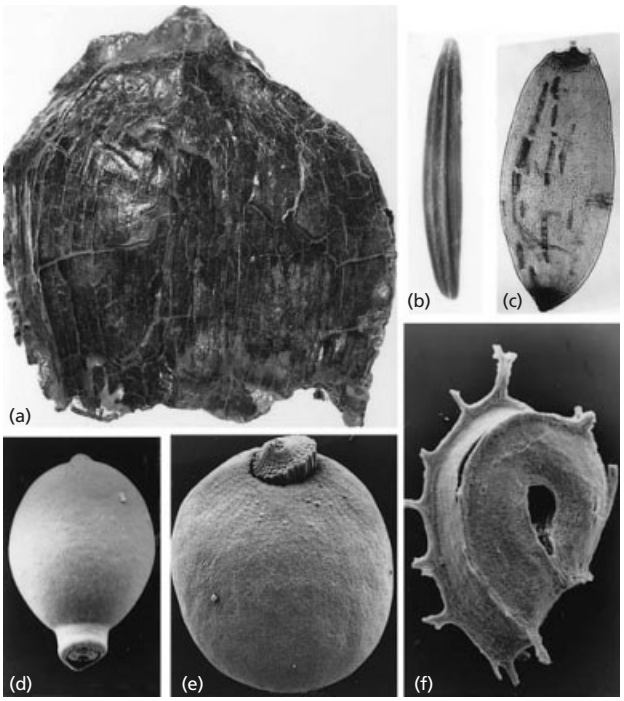

Fig. 1.5.3.1 Fossil fruits and seeds of flowering plants representative of *Nypa*-dominated mangrove (a,b) and freshwater marsh (c–f) in the Eocene. (a) Fruit of *Nypa* (mangrove palm), ×0.5. (b) Viviparous embryo of *Ceriops* (mangrove of the Rhizophoraceae family), ×1.5. (c) Seed of *Typha* (bulrush), ×35. (d) Seed of *Aldrovanda* (water wheel), a free-floating insectivorous plant with traps like those of Venus fly trap, ×15. (e) Seed of *Brasenia* (red water lily), ×20. (f) Fruit of *Potamogeton* (pond weed), ×40. See Section 4.1.18 for references to further details. (a,b, Reflected light micrographs; c, transmitted light micrograph; d–f, scanning electron micrographs.)

draceae (katsura and *Trochodendron* trees), Juglandaceae (walnuts and wingnut trees), Platanaceae (plane trees = sycamores in North America), and Ulmaceae (elm trees), as well as the *Ginkgo* (maidenhair tree) and conifers of the Taxodiaceae (swamp cypresses). The climate is judged to have been free from severe frost and with mild moist summers; deciduousness resulted from a lack of winter light rather than cold. All forest belts were shifted polewards at the Eocene thermal maximum but at other times (e.g. Late Paleocene) similar vegetation extended down into northern mid-latitudes (Alberta, Canada) where it existed as a deciduous forest colonizing open, disturbed areas of floodplains. There is no modern homologue of the polar deciduous forests because tree-dominated vegetation no longer exists at polar latitudes and this, albeit recent, biome is now extinct. However, the plants which once grew in the polar deciduous forests occur today in mesothermal to warm microthermal, broadleaved deciduous and mixed conifer/broadleaved deciduous forests in mid-latitudes in various parts of the world (Collinson 2000). Other elements in these modern deciduous forests may have originated in upland areas during the Eocene. Microthermal, broadleaved deciduous forests similar to those of the present day occupied mid-latitudes following the terminal Eocene temperature decline, though some mesothermal elements persisted in places. More arid floral elements appeared in continental interiors and forest canopies were lost, resulting in an opening of habitats which intensified during the Miocene (Collinson 1990, 2000; Wing 1998).

Conifer forests

Modern conifers are known in Mesozoic and Cenozoic floras but conifer forest comparable to the taiga in the boreal realm today (very low diversity to monotypic) is not documented in Palaeogene floras. Pinaceae conifers increased in the Late Eocene to Oligocene floras of northern high latitudes (see deciduous forests above) and through the Neogene conifers became increasingly important in these forests (Collinson 1990, 2000); boreal conifer forest is documented in the latest Pliocene of North America (Wing 1998).

Wetlands

Peat-forming, tree-dominated wetlands (swamp forests), like those of the present day in south-eastern USA, dominated by Taxodiaceae (swamp cypresses), occurred in the Late Cretaceous and early Tertiary (Collinson 1990). In the Miocene the peat-forming habitats which produced the extensive European brown coals included several distinguishable modern subcommunities, such as *Taxodium* swamp, *Nyssa* swamp, and *Cyrilla* shrub (Collinson 2000). Herb-dominated wetlands, with many floral similarities to those of the southern USA today, are also documented in the latest Paleocene and Eocene. These are especially well known in the English Late Eocene and included modern wetland associations such as a *Typha* (Fig. 1.5.3.1c) and *Acrostichum* (bulrush and leather fern) marsh, as well as marginal, open-water rooted, and free-floating aquatics such as water lilies (Fig. 1.5.3.1e), pond weeds (Fig. 1.5.3.1f), water wheel (Fig. 1.5.3.1d), water soldier, bur read, arrowheads, sedges, and water ferns with distinctive subcommunities at different sites (Collinson and Hooker *in* Friis *et al.* 1987; Hooker *et al.* 1995).

Herb-dominated (non-aquatic) vegetation

Although early flowering plants are considered to have been herbs or shrubs (Wing and Boucher 1998), these were very different from modern examples like the grasses and meadowland herbs. Important groups of

flowering plant herbs, such as subclasses Liliidae (lilies), Asteridae (e.g. daisies), and Caryophyllidae (e.g. pinks), and also several groups of Dilleniidae (cresses, umbellifers), show evident diversification only in the late Neogene or later (Collinson *et al*. *in* Benton 1993; Collinson 2000). Herb-dominated vegetation is a Late Miocene to Pliocene or Pleistocene development. Boreal forests persisted in many areas (e.g. borders of the Arctic Ocean) until the Pleistocene; tundra and true open grassland probably never existed in the Neogene (see Section 1.5.1) (Wing 1998; Collinson 2000).

Overview

The rise of modern land biomes, dominated by flowering plants, mammals, birds, and insects, is essentially a Cenozoic phenomenon. Modern herbaceous vegetation (including grasslands), and modern low-diversity to monotypic, boreal, conifer forest (taiga), had their origins in the late Neogene or later. Neogene vegetation contained plant subcommunities which can still be recognized at the present day. Palaeogene vegetation, in contrast, often contained combinations of plant genera whose nearest living relatives are now segregated in different geographical areas, and/or have small relict distributions, due to later Cenozoic climate change (especially global cooling). An important Eocene vegetation, polar broadleaved deciduous forest, is now extinct but near relatives of its component plants survive (alongside other taxa) in modern, mid-latitude, deciduous forests. Eocene tropical forests and *Nypa*-dominated mangroves extended to around 55–65° N and S. The tropical forests shared many features with the vegetation of modern tropical rain forests, but differed in the apparent absence of flowering plant epiphytes and in the lack of some key plant taxa. Eocene *Nypa*-dominated mangroves, and freshwater wetland swamps and marshes, were very similar to comparable modern vegetation.

References

Benton, M.J. (1993) *The fossil record 2*. Chapman and Hall, London.

Collinson, M.E. (1990) Plant evolution and ecology during the early Cainozoic diversification. *Advances in Botanical Research* **17**, 1–98.

Collinson, M.E. (2000) Cenozoic evolution of modern plant communities and vegetation. In: S.J. Culver and P.F. Rawson, eds. *Biotic response to global change: the last 145 million years*, pp. 223–243. Cambridge University Press, Cambridge.

Collinson, M.E. and Hooker, J.J. (1991) Fossil evidence of interactions between plants and plant-eating mammals. *Philosophical Transactions of the Royal Society of London B* **333**, 197–208.

Friis, E.M., Chaloner, W.G. and Crane, P.R. (1987) *The origins of angiosperms and their biological consequences*. Cambridge University Press, Cambridge.

Hooker, J.J., Collinson, M.E., van Bergen, P.F., Singer, R.L., de Leeuw, J.W. and Jones, T.P. (1995) Reconstruction of land and freshwater palaeoenvironments near the Eocene–Oligocene boundary, southern England. *Journal of the Geological Society of London* **152**, 449–468.

Krings, M. and Kerp, H. (1999) Morphology, growth habit and ecology of *Blanzyopteris praedentata* (Gothan) nov. comb., a climbing neuropteroid seed fern from the Stephanian of central France. *International Journal of Plant Science* **160**, 603–619.

Lupia, R., Crane, P.R. and Lidgard, S. (2000) Angiosperm diversification and Cretaceous environmental change. In: S.J. Culver and P.F. Rawson, eds. *Biotic response to global change: the last 145 million years*, pp. 207–222. Cambridge University Press, Cambridge.

Morley, R.J. (2000) *Origins and evolution of tropical rain forests*. Wiley, London.

Wing, S.L. (1998) Tertiary vegetation of North America as a context for mammalian evolution. In: C.M. Janis, K.M. Scott and L.L. Jacobs, eds. *Evolution of Tertiary mammals of North America*, Vol. 1, pp. 32–65. Cambridge University Press, Cambridge.

Wing, S.L. and Boucher, L.D. (1998) Ecological aspects of the Cretaceous flowering plant radiation. *Annual Review of Earth and Planetary Sciences* **26**, 379–421.

1.5.4 Early Primates

K.D. ROSE

Introduction

Living primates include monkeys, apes, and humans (grouped as anthropoids), and their primitive cousins the lemurs, lorises, and tarsiers (prosimians). This arrangement is gradistic but only partly phylogenetic: Anthropoidea are considered monophyletic, whereas prosimians are not. Consequently, many authorities employ the cladistic terms Strepsirrhini for lemurs + lorises (= Lemuriformes), and Haplorhini for Tarsiiformes + Anthropoidea (Fig. 1.5.4.1). A sister-taxon relationship between tarsiers and anthropoids is supported by genetics, placentation, cranial anatomy, and other criteria (Martin 1993; Kay *et al*. 1997; Fleagle 1999). However, other evidence has been adduced that strepsirrhines might be closer to anthropoids (Fleagle 1999). The closest relative of Anthropoidea thus remains one of the most contentious issues in primate systematics.

Undoubted forerunners of living primates—the oldest known strepsirrhines and tarsiiforms—can be traced back to the beginning of the Eocene (55 Ma). Equivocal

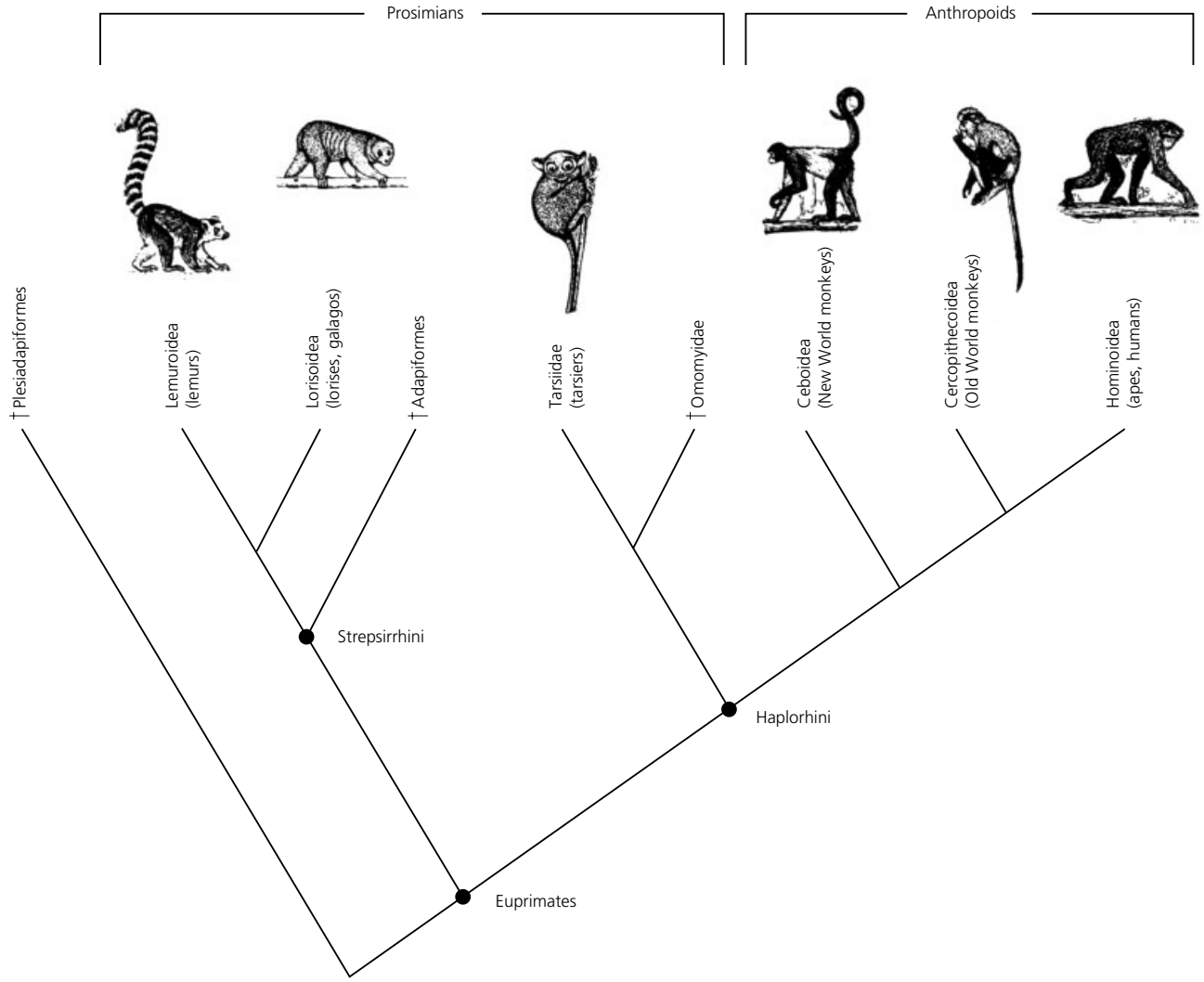

Fig. 1.5.4.1 Cladogram of relationships of the principal groups of living and extinct (†) primates.

primate relatives, comprising the order or suborder Plesiadapiformes, date back to the Early Paleocene (65 Ma).

Origin of Primates

Whether the order Primates is restricted to extant forms and their undisputed extinct relatives (= Euprimates), or encompasses Plesiadapiformes as well, the origin of the group is enigmatic. The oldest euprimates appear abruptly in the fossil record in basal Eocene deposits of North America and Europe (slightly later in Asia), with no clear indication of either their phylogenetic or geographical source. They seem to be part of an immigration event, also involving the ungulate orders Perissodactyla and Artiodactyla, that characterizes the Paleocene–Eocene boundary across Holarctica; but where these animals immigrated from is unknown. Because two euprimate clades are already present, a Paleocene or earlier origin of the order is indicated. Fragmentary dentitions of putative Late Paleocene euprimates are known from Morocco (*Altiatlasius*) and Mongolia (*Altanius*), but their relationships to other euprimates are controversial, and neither provides additional insight into euprimate origins (Rose 1995).

Early Eocene euprimates already possess anatomical traits diagnostic of living primates (Fig. 1.5.4.2b,c). The most important of these are a relatively large brain, a bony postorbital bar (a continuous bridge of bone around the lateral side of the eye socket), an auditory bulla (the thin, bubble-like, bony structure surrounding the middle ear cavity) composed of the petrosal bone, an opposable hallux (big toe), and digits with nails rather

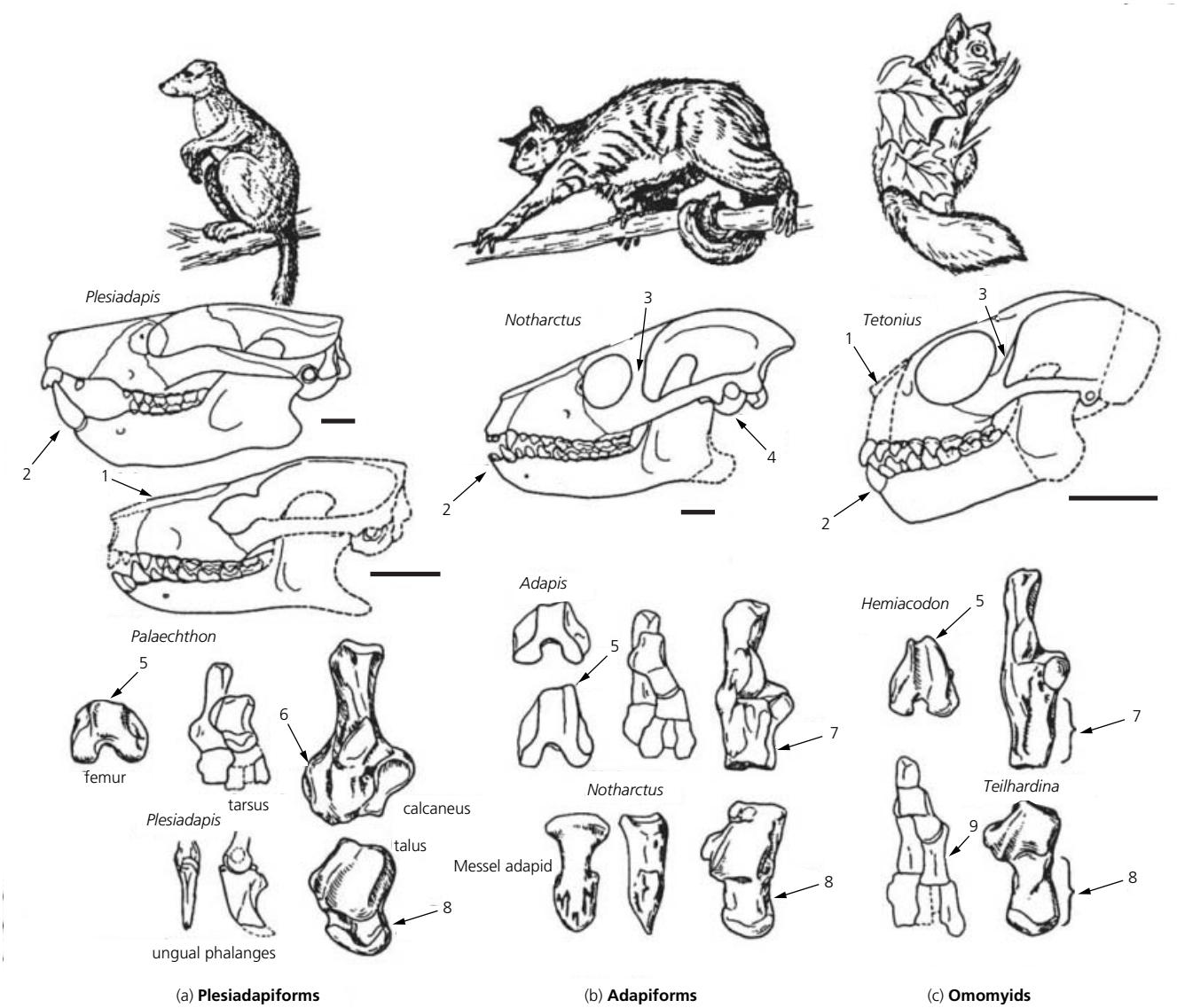

Fig. 1.5.4.2 Principal skeletal differences among: (a) plesiadapiforms; (b) adapiforms; and (c) omomyids. Lower drawings compare aspects of the distal femur, tarsus (ankle, with two ankle bones, the calcaneus and talus, enlarged), and ungual phalanges (terminal finger or toe bones, in dorsal and lateral view). Drawings in (a) are of *Plesiadapis*, except for lower skull (*Palaechthon*); those in (b) are mainly *Notharctus*, except for upper femur (*Adapis*) and ungual phalanges (unidentified adapid); in (c), skull and restoration represent *Tetonius*, lower left drawings are of *Hemiacodon*, and lower right drawings are of *Teilhardina*. Arrows highlight characteristics of each group: in the skull these include (1) snout length, (2) incisor size and form, (3) presence of postorbital bar, and (4) structure of auditory bulla; postcranial features include (5) configuration of patellar groove (the joint surface on the distal femur for the patella, or knee cap), (6) size of calcaneal peroneal tubercle (a bony process on the heel bone), and distal elongation of ankle bones, calcaneus (7), talus (8), and navicular (9). Scale bars for skulls = 1 cm. (From Rose 1995; reprinted by permission of Wiley-Liss, Inc., a subsidiary of John Wiley & Sons, Inc.)

than claws. These features probably arose as adaptations to arboreal life, and perhaps to visually orientated predation, but the exact explanation is not understood, and transitional stages that would document how they evolved from more generalized states are unknown.

The only Paleocene mammals that show modifications in the direction of primates are Plesiadapiformes, so-called 'archaic primates'. Plesiadapiforms have conventionally been included in Primates, usually as a suborder (Rose 1995; Fleagle 1999). Their precise relationship to euprimates is unknown, however, and some experts dispute any special relationship at all.

Postcranial specializations for arboreality and modifications of the molar dentition similar to those of Eocene euprimates are often cited as evidence of common ancestry. Undeniably derived dental resemblances do exist, including low cusps and trigonids (the anterior half of the lower molars, consisting of three cusps), broad basined talonids (the posterior half of lower molars), expanded lower third molars, and narrow stylar shelves (the region of the upper molars between the two main external cusps and the buccal border of the tooth). Functionally, this dental complex suggests a shift from insectivory to a more omnivorous or herbivorous diet. However, some of the closest dental similarities exist between plesiadapiforms and euprimates that cannot be directly related—an indication that these resemblances arose through evolutionary convergence. Furthermore, the oldest euprimates retain four lower premolars, whereas all except the two most primitive known plesiadapiforms (*Purgatorius* and *Anasazia*) have lost the first premolar. Thus only these two plesiadapiforms could be directly related to the origin of Euprimates. In addition, the fact that plesiadapiforms (Fig. 1.5.4.2a) lack many of the diagnostic traits of Euprimates (Fig. 1.5.4.2b,c) has led to an increasing rejection of their inclusion in Primates (Martin 1993).

The origin of Plesiadapiformes is also obscure, because most are known only from dentitions, and knowledge of potential Cretaceous precursors is so limited. Dental morphology suggests affinities with erinaceomorph insectivorans, which differ from other insectivores in having lower-crowned teeth with less acute cusps and broad talonid basins. Other anatomical evidence does not support this relationship, however, leaving the question of plesiadapiform origins unresolved.

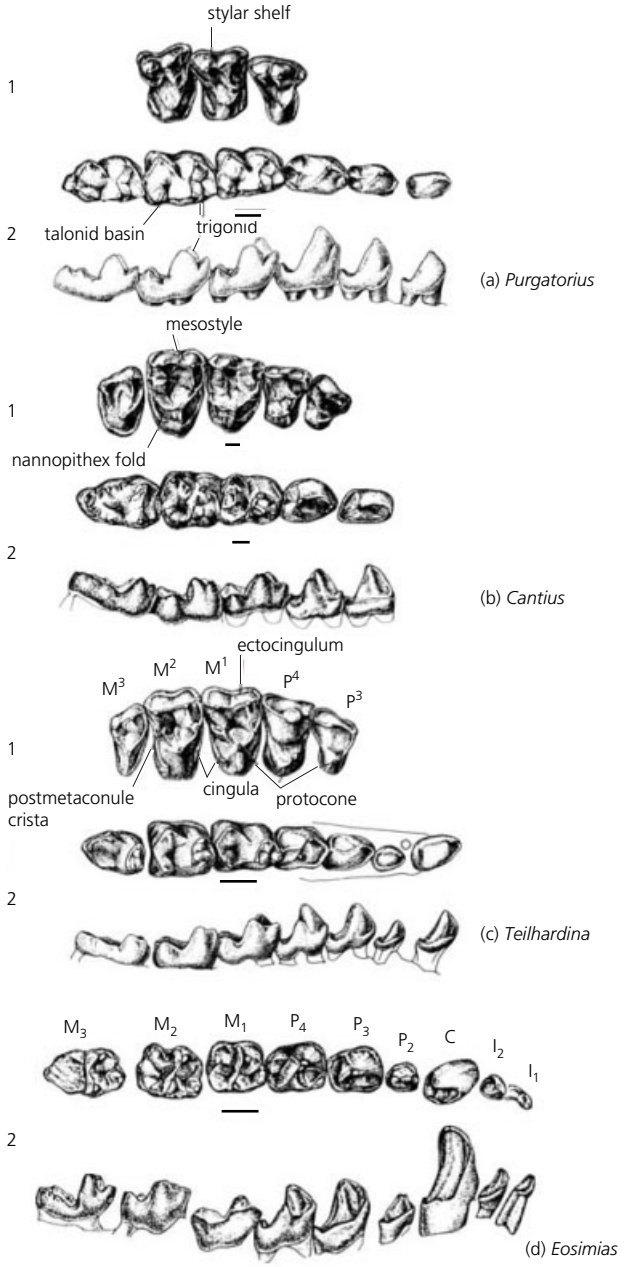

Fig. 1.5.4.3 Comparison of right upper (1) and left lower (2) dentitions of: (a) *Purgatorius* (plesiadapiform); (b) *Cantius* (adapiform); (c) *Teilhardina* (omomyid); and (d) *Eosimias* (anthropoid). Scale bars = 1 mm. (Modified from Rose 1995; reprinted by permission of Wiley-Liss, Inc., a subsidiary of John Wiley & Sons, Inc.)

Plesiadapiformes

Plesiadapiforms were mouse- to marmot-sized arboreal animals that were among the most successful Paleocene–Eocene mammals. They were especially common and diverse in western North America, and are also known from Eurasia. Plesiadapiforms occupied an ecological niche approximating to that of Eocene rodents and euprimates. All three groups coexisted in the Eocene, but plesiadapiforms were considerably less speciose and abundant then than during the Paleocene, a decline attributed to competition with rodents (Fleagle 1999).

Early Paleocene *Purgatorius* (Fig. 1.5.4.3a) from western North America is the oldest and most primitive plesiadapiform. Only its dentition is known, which resembles that of later plesiadapiforms in the characters listed earlier, except for having sharper cusps. The lower dental formula—3 incisors, 1 canine, 4 premolars, and 3 molars (abbreviated as 3-1-4-3)—is the most primitive known for Plesiadapiformes. (Almost all later plesiadapiforms lost at least one incisor and one premolar.) *Purgatorius* or a similar form probably lies near the ancestry of all other plesiadapiforms (Rose 1995; Fleagle 1999).

There are 10 families of plesiadapiforms, six of

which were established by the late Early Paleocene (Torrejonian North American Land-Mammal Age). Besides Purgatoriidae, they include Palaechthonidae, Plesiadapidae, Carpolestidae, Paromomyidae, and Picrodontidae. Four additional families appear in Late Paleocene or Early Eocene sediments: Saxonellidae, Micromomyidae, Microsyopidae, and Picromomyidae. Most of the more than 90 species and 40 genera are known solely or primarily from dentitions. Plesiadapiforms ranged in size from shrew-sized *Picromomys* (10 g) to marmot-sized larger species of *Plesiadapis* (3–5 kg).

The skull tends to have a long snout, laterally directed orbits, no postorbital bar, and a small braincase (Fig. 1.5.4.2a). Composition of the auditory bulla is difficult to establish with certainty, but in *Ignacius* (Paromomyidae) it seems to consist of the entotympanic bone, in contrast to the petrosal bulla of euprimates (Martin 1993). The endocranial arterial pattern also differs from that of the euprimates (and resembles that of Dermoptera) in lacking any significant blood supply from the internal carotid artery. Most plesiadapiforms had conservative molars and many had specialized antemolar dentitions. All had a pair of enlarged, procumbent (inclined) lower central incisors, which typically occluded with large, multipronged upper incisors. Parallel dental specializations were common. Reduction in the number or size of anterior teeth behind the incisor occurred in several lineages, and some (Plesiadapidae, Paromomyidae) developed an edentulous diastema (gap) between the incisor and posterior premolars. An enlarged, pointed, last lower premolar (P_4) evolved independently in paromomyids and micromomyids, and a bizarre, multicusped premolar blade arose separately in carpolestids (where it was P_4) and saxonellids (P_3). Sharp molar cusps and crests and the diminutive body size of some plesiadapiforms suggest they were insectivorous, whereas larger species (Plesiadapidae) have dental modifications indicative of omnivory or herbivory (including fruit and seed-eating). In other lineages (Paromomyidae, Picrodontidae, Picromomyidae), flatter molars coupled with procumbent incisors suggest gum feeding.

The postcranial skeleton is known in only three families (Plesiadapidae, Paromomyidae, and Micromomyidae), and only for *Plesiadapis* is it almost completely known. *Plesiadapis* had a relatively robust skeleton bearing the anatomical hallmarks of arboreal adaptation (strong crests and processes on limb elements, mobile elbow and ankle joints, sharp, laterally compressed claws). The lack of further specializations indicates that *Plesiadapis* was a non-acrobatic arboreal quadruped.

In contrast, paromomyids and micromomyids had more delicate limb bones with modifications of ankle, wrist, and digits that resemble those of living dermopterans and suggest the presence of a patagium, or gliding membrane. These and certain cranial features have been considered synapomorphies linking these families with Dermoptera (Beard 1993). This hypothesis has been challenged, however (see Martin 1993). Among conflicting evidence is the fact that paromomyid and micromomyid dentitions differ significantly from those of extant dermopterans. The controversy is likely to persist until there is more compelling evidence for or against a plesiadapiform–dermopteran relationship.

Euprimates

The oldest unequivocal primates appear suddenly at the beginning of the Eocene in Europe and North America. They already represent two major prosimian clades, Adapiformes and tarsiiform Omomyidae, which reflect the primary euprimate dichotomy into Strepsirrhini and Haplorhini (Fig. 1.5.4.1). Early euprimates were common mammals in Eocene assemblages. About 65 genera and 150 species of adapiforms and omomyids are currently recognized—triple the number of taxa of extant prosimians. Eocene euprimate lineages provide some of the best documentation known for gradual evolution (Rose 1995; Fleagle 1999).

Adapiformes

Among the best known of all fossil primates, adapiforms are represented by dozens of skulls, several nearly complete skeletons, and thousands of jaws. Anatomical evidence indicates that Adapiformes is the sister-group of living Strepsirrhini. Eocene representatives belong to two holarctic families: the lemur-like Notharctidae (best known from North America); and the somewhat loris-like (mainly European) Adapidae. Most of the more than 30 genera and 75 species of adapiforms are now regarded as notharctids, and European species outnumber North American ones; adapiforms are also known from Asia and North Africa (Godinot 1998).

Skeletons of notharctids, best known for North American *Notharctus* (Fig. 1.5.4.2b) and *Smilodectes* and European *Europolemur*, resemble in size and anatomy those of extant leaping arboreal lemurs. The hindlimbs were markedly longer than the forelimbs, the joints very flexible, and the feet adapted for grasping (with an opposable hallux and nails rather than claws). *Adapis* and *Leptadapis*, the best-known adapids, lack leaping specializations and instead show limb modifications that indicate either slow arboreal progression (like lorises) or perhaps quadrupedal running. The skull of most adapiforms was long-snouted, with small orbits, suggesting diurnal activity patterns. Short-snouted *Pronycticebus* had larger orbits, however, suggesting nocturnality (Godinot 1998). Some types were sexually dimorphic, judging by the strong sagittal crest and large canine teeth

of some specimens (presumably males). Most adapiforms weighed 1–5 kg, though some species were smaller than 100 g and others as large as 7 kg (Godinot 1998; Fleagle 1999).

European *Donrussellia* and Euramerican *Cantius* (Fig. 1.5.4.3b) are the most primitive known adapiforms. Like many other adapiforms, they retain a primitive dental formula (2-1-4-3). Adapiform molars had either low, rounded cusps adapted for frugivory, or sharp crests specialized for leaf-eating. Some small species had sharper cusps and must have been partly insectivorous. Adapiforms had small, vertical or somewhat inclined incisors and projecting canines (Fig. 1.5.4.2b; they lacked the lower toothcomb characteristic of living strepsirrhines.

Tarsiiformes

The Omomyidae, consisting of about 35 genera and 80 species, were the most successful and diverse radiation of tarsiiform primates. They are generally considered to be closely allied with, or ancestral to, Tarsiidae. Omomyids flourished in the Eocene and were most common and diverse in North America, but they also lived in Europe, Asia, and North Africa. Most omomyids were an order of magnitude smaller than contemporary adapiforms, weighing 100–500 g, but a few species reached 1–2 kg (Fleagle 1999).

The most primitive omomyids, Euramerican *Teilhardina* (Fig. 1.5.4.3c) and North American *Steinius*, had the same lower dental formula as in basal adapiforms (2-1-4-3), and the teeth show only subtle differences from those of *Donrussellia*, corroborating close common ancestry. Other omomyids lost at least the first premolar. Here, too, parallelism was common, and many lineages independently evolved enlarged, procumbent medial incisors, and tall, pointed lower fourth premolars. Based on small size and moderately sharp molar cusps, as in *Tarsius*, most omomyids are inferred to have been partly insectivorous. Some species probably also consumed gum, and larger species with more rounded cusps or crenulated enamel were presumably frugivorous or folivorous.

Although most omomyid species are represented only by dentitions, skulls are known for a few genera (*Tetonius*, *Shoshonius*, *Necrolemur*). They had short faces and distinctly larger orbits than adapiforms (but much smaller than *Tarsius*), suggesting nocturnality (Fig. 1.5.4.2c). Late Eocene *Rooneyia*, however, had relatively smaller orbits and was probably diurnal. The few known postcranial remains indicate that omomyids were active arboreal leapers with tarsal elongation comparable to that of living galagos, rather than the extreme elongation of *Tarsius* (Fig. 1.5.4.2c).

Two omomyid genera, *Necrolemur* and *Shoshonius*, have been considered particularly close to tarsiid origins, but dentitions recently discovered in China demonstrate that tarsiids very similar to extant *Tarsius* existed by Middle Eocene time (Beard *et al.* 1994). Hence Tarsiidae may be as ancient as Omomyidae and Adapiformes.

Origin of Anthropoidea

The source of Anthropoidea is an issue of intense debate, fuelled by exciting new fossil evidence from North Africa and China. Specialists are divided as to whether Anthropoidea are more closely related to Adapiformes or Tarsiiformes. Anatomical features can be cited in support of either argument, but a truly compelling case that would exclude one of these alternatives has yet to be made. It is also possible that anthropoids represent a third major clade tracing back to the origin of Primates. One conclusion that seems indisputable is that Anthropoidea evolved much earlier than previously thought.

The richest record of early anthropoids comes from Late Eocene–Early Oligocene deposits of Egypt, which have produced 10 genera of primitive anthropoids, including *Aegyptopithecus*, *Apidium*, and *Catopithecus* (Simons 1995; Fleagle 1999). Teeth, skulls, and postcranial skeletons confirm their anthropoid status, and also demonstrate that anatomical features diagnostic of Anthropoidea evolved in mosaic fashion. These early anthropoids were diurnal arboreal quadrupeds that fed on fruits and seeds. *Apidium* was also adapted for leaping (Simons 1995).

Discoveries in Algeria (*Algeripithecus*) and China (*Eosimias*, Fig. 1.5.4.3d) potentially push back the record of Anthropoidea 10 myr to at least the Middle Eocene (Martin 1993; Beard *et al.* 1994). Although these animals possess certain anthropoid features, they are decidedly more primitive in other traits. Confident assessment of their relationship to Anthropoidea must await more complete fossils; existing data suggest that *Eosimias* is the sister-taxon either of Anthropoidea or of Haplorhini.

References

Beard, K.C. (1993) Phylogenetic systematics of the Primatomorpha, with special reference to Dermoptera. In: F.S. Szalay, M.J. Novacek and M.C. McKenna, eds. *Mammal phylogeny: placentals*, pp. 129–150. Springer-Verlag, New York.

Beard, K.C., Qi, T., Dawson, M.R., Wang, B. and Li, C. (1994) A diverse new primate fauna from middle Eocene fissure-fillings in southeastern China. *Nature* **368**, 604–609.

Fleagle, J.G. (1999) *Primate adaptation and evolution*, 2nd edn. Academic Press, San Diego.

Godinot, M. (1998) A summary of adapiform systematics and phylogeny. *Folia Primatologica* **69** (Suppl. 1), 218–249.

Kay, R.F., Ross, C. and Williams, B.A. (1997) Anthropoid origins. *Science* **275**, 797–804.
Martin, R.D. (1993) Primate origins: plugging the gaps. *Nature* **363**, 223–234.
Rose, K.D. (1995) The earliest primates. *Evolutionary Anthropology* **3**, 159–173.
Simons, E.L. (1995) Egyptian Oligocene primates: a review. *Yearbook of Physical Anthropology* **38**, 199–238.

1.5.5 Hominid Evolution

B.A. WOOD

Introduction—Man's closest relatives

There is anatomical, molecular, and genetic evidence that the close relatives of modern humans are *Pan* (chimpanzee) and *Gorilla*. More detailed analyses of the DNA in both the nucleus and the mitochondria have revealed many similarities between the genomes of *Homo sapiens* and *Pan*, and an increasing number of researchers are convinced that *Homo* and *Pan* share a common ancestry to the exclusion of *Gorilla* (Ruvolo 1997). Most mutations are neutral, and if it is assumed that these neutral mutations have been occurring at the same rate in closely related lineages, then the degree of molecular difference can be used as a 'clock' to estimate the time elapsed since any two lineages separated. When this is done for the molecular differences between modern humans and the living African apes, it has been estimated that the human and chimpanzee lineages separated between 8 and 5 Ma (Fig. 1.5.5.1). Animals that are judged to be more closely related to modern humans than to the apes are called 'hominids'. What is known about the emergence and subsequent evolutionary history of this lineage?

Ancestral differences

The list of morphological differences between modern humans and the chimpanzee is an impressive one, but the differences between the earliest hominids and the Late Miocene ancestors of the living great apes are likely to have been a good deal more subtle. Those who study human evolution have to focus on the features that distinguish modern humans and the living apes and then trace these back into human prehistory. Some of these features, such as those linked with bipedalism, can be traced back a long way. Others, such as the relatively diminutive jaws and chewing teeth of modern humans, were acquired more recently, and thus cannot be used to discriminate between early hominids and potential ape ancestors. The presumption has been that ape ancestors will be quadrupeds with projecting faces accommodating elongated jaws, bearing relatively small chewing teeth and large, sexually dimorphic, canine teeth. Early hominids, on the other hand, will be distinguished by cranial and other skeletal adaptations to a predominantly upright posture, and skeletal and other adaptations for a locomotor strategy that includes substantial bouts of bipedalism, together with a masticatory apparatus which combines relatively large chewing teeth and modest-sized canines. However, these are hypotheses which may have to be revised as more fossil evidence is recovered from the 8–5 Ma interval.

Ardipithecus—the earliest hominid?

The hominoid fossil record for the period 8–5 Ma is poor, consisting of isolated specimens, most of which are too fragmentary to provide any reliable evidence about taxonomic affinity. The first creature with a more comprehensive fossil record, and which shows at least some rudimentary human specializations, is *Ardipithecus ramidus*, the 4.5 Ma remains of which were recovered at a site called Aramis, Ethiopia, in 1992 and thereafter. The fossils share some features with living species of *Pan*, others with the African apes in general, and, crucially, several features of the skull and teeth with later hominids. The material was initially allocated to an established genus, *Australopithecus*, but its describers have subsequently assigned it to a new genus, *Ardipithecus*. It is claimed (White *et al.* 1994) that the canines of *A. ramidus* are relatively larger, the crowns of the first deciduous molars are less complex, the articular eminence is flatter, the enamel is thinner, and that both the upper and the lower premolar crowns are more asymmetric, and thus more ape-like, than the equivalent morphology in *Australopithecus afarensis*, the taxon that was previously believed to have been the most primitive hominid. *Ardipithecus ramidus* should be excluded from the apes because of the relatively small upper central incisors, the lack of a well-defined canine honing mechanism, the broad mandibular molar crowns, and because the foramen magnum is situated too far anteriorly.

Judging from the size of the shoulder joint, *A. ramidus* weighed ≈ 40 kg. Its chewing teeth were relatively small and the position of the foramen magnum (the opening for the spinal cord) was close to the centre of the skull, suggesting that the posture and gait of *A. ramidus* were, respectively, more upright and bipedal than is the case in the living apes.

The context of *A. ramidus* suggests that the bones were buried close to, if not actually within, woodland. Neither the size of the brain, nor the nature of the posture and locomotion are yet known. The thin enamel covering on

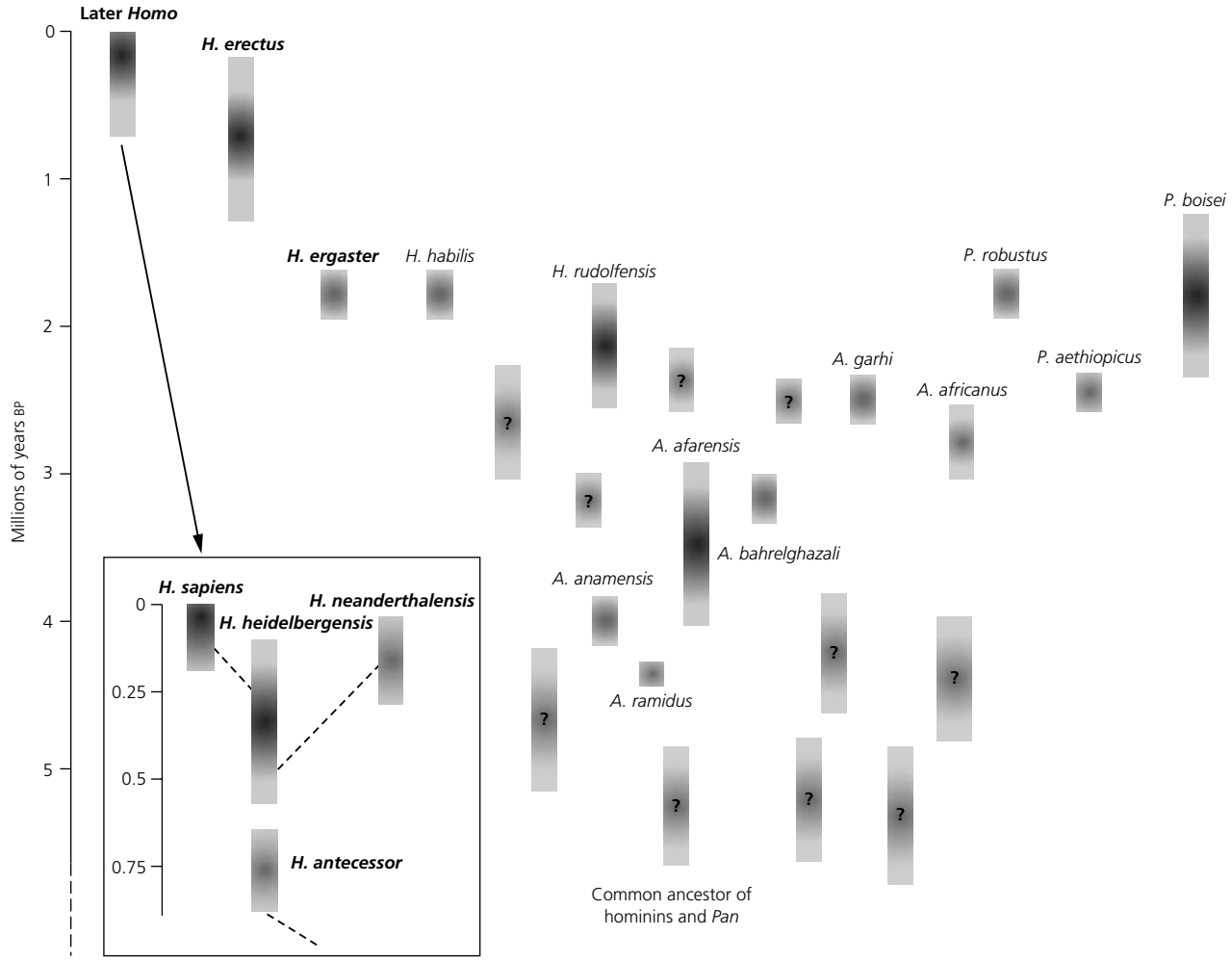

Fig. 1.5.5.1 Phylogram showing the species of hominids. Many now place these taxa in the tribe Hominini, instead of the family Hominidae (see Table 1.5.5.1). Thus the species are referred to as hominins, as opposed to chimpanzees and their direct ancestors, or panins. The horizontal axis spreads the species out according to the relative size of their chewing teeth and brain size; taxa with large molar and premolar crowns are to the right, and those with smaller postcanine teeth are to the left. Of the early taxa, the best evidence for brain enlargement comes from *Homo habilis*. The brain of *H. ergaster* (≈ 850 cm^3) is absolutely, but not relatively, larger than *H. habilis* (≈ 550 cm^3) because the former is estimated to have a larger body mass. Recently, it has been suggested that *H. habilis* and *H. rudolfensis* are more closely related to *Australopithecus* than to *Homo*, thus the genus *Homo* should probably be restricted to the taxa in **bold** type. The hypothetical taxa are a reminder that the period between 2 and 6 Ma is relatively poorly sampled, and that, if the experience of the Pleistocene is repeated, the numbers of species and genera will almost certainly increase. For generic abbreviations, see Table 1.5.5.1.

the teeth suggests that the diet of *A. ramidus* may have been closer to that of the chimpanzee than is the case with any of the other early hominids.

Australopithecus

Approximately half a million years later in time, also from east African sites, there is much better preserved evidence of another primitive hominid, *Australopithecus afarensis*. This was the name given in 1978 to hominid fossils recovered from Laetoli, in Tanzania, and from the Ethiopian site of Hadar. Since then further evidence of *A. afarensis* has been found at other localities in Ethiopia, and in Kenya. The majority of this evidence is dated to between 4 and 3 Ma.

The fossil record of *A. afarensis* includes a well-preserved skull, substantial portions of several others, many lower jaws and limb bones, as well as just less than half of an adult female skeleton. The picture that emerges is of a species that ranged in body mass from about 25 kg for a small female, to more than 50 kg for a large male. This is a substantial size range for an animal

so small, and some workers have revived the suggestion that *A. afarensis* may consist of the remains of more than one species of early hominid.

The brain volume of *A. afarensis* was between 400 and 500 cm^3, but relative to its estimated body mass the brain is no larger than that of the chimpanzee. However, the chewing teeth—the premolars and molars—are relatively larger than those of the contemporary apes.

Reconstructions of the habitat of *A. afarensis* suggest that it lived in an 'open' woodland environment. The appearance of the pelvis and the lower limb suggests that, although *A. afarensis* was capable of bipedal walking, it was not adapted for long-range bipedalism. This indirect evidence for the locomotion of *A. afarensis* is complemented by the discovery, at Laetoli, of several trails of fossil footprints. These provide direct evidence that *A. afarensis* was capable of bipedal locomotion. The size of the footprints and the length of the stride provide corroboration for estimates of stature derived from the limb bones of *A. afarensis*. These suggest that its standing height was between 1 and 1.5 m.

Fossils dating to between 4 and 4.5 Ma have been found at Kanapoi in northern Kenya. In some ways these resemble *A. afarensis*, but in others they are more primitive, and they have been placed in a separate species, *Australopithecus anamensis*. A third species, *Australopithecus bahrelghazali*, was introduced for 3.5 Ma hominid remains from Chad, in north central Africa, and the most recent evidence for *Australopithecus* in east Africa are the 2.5 Ma remains of *A. garhi* (Asfaw *et al.* 1999).

Discoveries in southern Africa

Nearly 50 years before the discovery of *A. afarensis*, a child's skull was found in 1924 at the Buxton Limeworks in Taung, southern Africa. The exact geological age of the find was not known, but it was more primitive than any of the hominid remains that had been recovered previously in Europe, Java, or China. In 1925 the new hominid was named *Australopithecus africanus*, which literally means the 'southern ape' of Africa.

Since the Taung discovery, the remains of *A. africanus* have been found at other cave sites in southern Africa, at Makapansgat and Gladysvale, but at present these sites can only be dated by comparing the remains of the mammals found in the caves with the mammalian fossils found at the better-dated sites in east Africa. In this way the *A. africanus*-bearing cave breccias have been estimated to be between 2.4 and 3 Ma.

Males and females of *A. africanus* probably did not differ in body size to the degree they did in *A. afarensis*. The physique of *A. africanus* was much like that of *A. afarensis*, except that its chewing teeth were larger and the skull was not as ape-like. The brain was larger than that of *A. afarensis* and the postcranial skeleton suggests that, although *A. africanus* was capable of walking bipedally, such a gait would have been relatively inefficient. The other animal remains found with *A. africanus* suggest that its habitat was a combination of grassland and trees, comparable to modern open 'bushland'.

Paranthropus—a genus of large-toothed hominids

Just as there are east and southern African regional variants of *Australopithecus*, there are two regional variants of another hominid genus called *Paranthropus*. They are often referred to as 'robust' australopiths because they have more massive faces and lower jaws than *Australopithecus* species.

Remains of the southern variety, *Paranthropus robustus*, come from caves at Swartkrans, Kromdraai, Gondolin, and Drimolen and are dated to between 2 and 1.5 Ma. The face and chewing teeth are larger than those of *A. africanus*, yet the incisor teeth are smaller, suggesting that there were dietary differences. What little is known of the postcranial skeleton suggests that it was similar to *A. africanus*. Some workers point to differences between the fossils from Swartkrans and Kromdraai, and allocate the former material to a separate species, *Paranthropus crassidens*.

The east African 'species' of *Paranthropus* probably consists of not one but two species (Table 1.5.5.1). Both have large jaws and large chewing teeth, and the later species is very sexually dimorphic; the earlier species dates from 2.5 to 2.3 Ma, and the later one between 2.3 and 1.4 Ma. The earlier and more primitive species, *Paranthropus aethiopicus*, is known from a handful of specimens including a well-preserved cranium. It has a smaller brain, around 400–450 cm^3, a more ape-like face, and larger anterior teeth than does the later species, *Paranthropus boisei*. The type specimen of *P. boisei* is the OH 5 cranium; it was originally referred to the genus *Zinjanthropus*. The relatively large chewing teeth in the two species have prompted the suggestion that they were specialist feeders on a diet that required heavy mastication. What little information there is about their postcranial skeleton suggests that it was much like that of *Australopithecus*.

The inclusion of the one southern African and two east African 'robust' species in the same genus, *Paranthropus*, reflects the consensus that they resemble each other because they inherited their wide face, large jaws, and large chewing teeth from a common ancestor. What prompted the appearance of these large-toothed creatures first in east Africa, and then in southern Africa? Some palaeontologists point to analogous changes occurring in the masticatory apparatus of other large mammals, and have suggested that the common 'cause' may be a general shift to a drier climate that occurred

between 3 and 2 Ma. This 'climatic' explanation has been linked to a global cooling phenomenon, superimposed on the effects of 'local' uplift of the land surface in the two regions (Partridge *et al.* 1995).

Table 1.5.5.1 Classification of fossil hominids. There is no 'official' hominid taxonomy. Some researchers prefer to recognize more, rather than fewer, species. Other researchers set their species boundaries at a higher level of variation; these interpretations would not recognize the species marked in **bold** type. The genera, and the species names within each genus, are listed in order of their publication. Species not in their original genus are marked with an asterisk. Traditional classifications of the higher primates place the non-human taxa in the family Pongidae, and modern humans and their ancestors in a second family, the Hominidae. Hence apes were referred to as 'pongids', and humans and their ancestors as 'hominids'. Given the compelling molecular evidence that chimpanzees are more closely related to modern humans than they are to gorillas, a new classification was required that interprets Hominidae more inclusively. In one version of such a classification, the orangutan and gorilla both have their own subfamily, Ponginae and Gorillinae. Modern humans and chimpanzees make up a third subfamily, Homininae, that consists of two tribes, Panini for the chimpanzees, and Hominini for modern humans and their ancestors. Hominini is divided into two subtribes, Australopithecina and Hominina, the details of which are given below. In this scheme the taxa we now refer to as hominids would be 'hominins'.

Hominoidea
- Hominidae
  - Hominini
    - Australopithecina
      - *Australopithecus*
        - ***A. afarensis***
        - *A. africanus*
        - ***A. anamensis***
        - ***A. bahrelghazali***
        - *A. garhi*
      - *Paranthropus*
        - *P. robustus*
        - *P. boisei**
        - ***P. aethiopicus****
      - *Ardipithecus*
        - *A. ramidus*
    - Hominina
      - *Homo*
        - *H. sapiens*
        - ***H. neanderthalensis***
        - *H. erectus*
        - ***H. heidelbergensis***
        - *H. habilis*
        - ***H. ergaster***
        - ***H. rudolfensis****
        - ***H. antecessor***

Early *Homo*, or its precursors?

When Louis and Mary Leakey discovered the OH 5 cranium at Olduvai Gorge in 1959, it was perhaps natural to assume that hominids like OH 5 made the stone tools found in the same sediments, but discoveries made in the same year, and in the 1960s, challenged this assumption.

The new material included parts of the vault, or roof, of a skull, a fragment of lower jaw, and parts of a hand, foot, and lower leg. Although these specimens are fragmentary, researchers were convinced that the larger cranial capacity, smaller tooth size, and what were interpreted as advanced features of the limb bones made this hominid a stronger contender for the role of toolmaker than OH 5. Therefore, Louis Leakey and colleagues proposed that the new material be included within the genus *Homo*, as a new species, *Homo habilis*, which means 'handy man', or 'maker of the tools'. They justified the inclusion of *H. habilis* in *Homo* because, they claimed, it departed significantly from the morphology of *Australopithecus* and *Paranthropus* in the direction of later *Homo*. That consensus has since broken down in the face of convincing demonstrations that the cranium and postcranial skeleton are less human-like than the original researchers had concluded.

Specimens resembling the Olduvai *H. habilis* remains have since been recovered from the site of Koobi Fora, in northern Kenya. As this evidence accumulated, it became apparent that *H. habilis* was more variable than would be expected for a single species. This led to the proposal that part of the *H. habilis sensu lato* hypodigm belonged to a second species of 'early *Homo*', and this was called *Homo rudolfensis* (Wood 1992).

Present evidence suggests that *H. habilis sensu stricto* dates from just less than 2 Ma to around 1.6 Ma, whereas *H. rudolfensis* dates from perhaps as early as 2.5 Ma to 1.8 Ma. In the two 'early *Homo*' species the opening for the spinal cord is closer to the middle of the skull, and compared with *Australopithecus* the skull base is reduced in length and increased in width. The two 'early *Homo*' species differ in the form of the face. In *H. habilis sensu stricto* the face is reduced in width and the opening of the nose is sharply defined. The brain volume of *H. habilis* is around 500–700 cm^3, whereas the estimated brain volume for *H. rudolfensis* is in the order of 700–800 cm^3, with an average of 750 cm^3.

Overall, the case for including *H. habilis sensu stricto* and *H. rudolfensis* within *Homo* has weakened since *H. habilis* was first announced. However, by around 1.9 Ma there is good evidence from East Africa of an early hominid that is a much stronger candidate for inclusion in *Homo* (Wood and Collard 1999).

Homo emerges in Africa

The painstaking excavation of a juvenile male skeleton, KNM-WT 15000, from one-and-a-half million years old sediments at West Turkana (Brown *et al.* 1985), had a significant effect on the interpretation of the early stages of the genus *Homo*. Over the previous decade, similar-looking skulls, jaws, and limb bones had been recovered from Koobi Fora, on the east side of Lake Turkana (Wood 1991). Although they resembled *Homo erectus* remains from Asia and elsewhere in Africa (see below), it was not until the discovery of KNM-WT 15000 that their affinities with each other and with *H. erectus* could be confirmed. Although the age of the West Turkana skeleton is ≈1.5 Ma, other remains attributed to the same species are as old as 1.9 Ma. Some workers have given the species a new name, *Homo ergaster*, while others refer to it as 'early African' *H. erectus*. Why are researchers more confident that these remains should be included in the genus *Homo*?

Homo sapiens differs from *Ardipithecus*, *Australopithecus*, and *Paranthropus* in four main ways. First, our brains are larger, both in absolute size and when they are related to the size of the body. Second, our jaws and teeth are generally smaller when related to body mass. Third, while it is apparent that the early hominids were capable of standing and even walking bipedally, the shape of their skeleton suggests that they could also still climb using all four limbs; they were not committed to bipedalism. Modern humans, on the other hand, only move from one place to another on all fours in childhood; adult modern humans are not only habitually upright in their posture, but they can only cover distances effectively if they are bipedal. The fourth distinction between modern humans and the early hominids, and particularly *Australopithecus*, is that whereas the early hominids and the apes accomplish their development relatively quickly, modern human infants are relatively helpless for longer, their locomotor skills take longer to acquire, and their molar teeth erupt later. This prolonged period of dependence, together with improved dexterity, is believed to have been important for the transfer of complex skills.

The remains of *H. ergaster*, or 'early African' *H. erectus*, satisfy most of these criteria. The lengths of the long bones of the skeleton from West Turkana confirm that this hominid species had a body shape and limb proportions more like those of modern humans. When the jaws and teeth of *H. ergaster* are related to body mass, they are no larger than those of African and Australian samples of modern humans. Likewise, the timing and pattern of tooth development in *H. ergaster* is much closer to that in modern humans than is the case for any of the other early hominid species. The cranial capacity of *H. ergaster*, between 800 and 900 cm^3, is greater than that of *H. rudolfensis*, but its relative size compared to body mass is similar.

Thus, the overall body plan of *H. ergaster* shows clear and strong links with modern humans. These resemblances are sufficient evidence to make *H. ergaster*, or 'early African' *H. erectus*, the first and earliest species which can confidently be placed within *Homo* (Wood and Collard 1999).

Homo expands beyond Africa

The first hominid species for which there is compelling evidence outside Africa is *Homo erectus*. More than a century ago Eugene Dubois reported the discovery of a skull and femur on the bank of the Solo River, at Trinil, in what is now Indonesia. Since then, similar-looking remains have been located elsewhere in Indonesia, mainly from the Sangiran region where the Solo River cuts through Pliocene and Pleistocene sediments.

Due to intensive cultivation, the exact location of many of the finds is difficult to pinpoint, and the paucity of volcanic ash and the weakness of the magnetic signals in the sediments means that accurate dating is difficult. There is, however, evidence that some of the finds at Sangiran may be around 1 Ma, and fossils from at least one of the sites may be ≈ 1.8 Ma (Swisher *et al.* 1994). The first hominids must have left Africa before this, and the first species to do so was likely to have been a *H. ergaster*-like hominid, or a more primitive precursor.

What prompted this first exodus from Africa? The larger bodies of *H. ergaster* would have provided improved tolerance to heat stress and to dehydration, and the more sophisticated stone 'tool kits' that make their first appearance around 1.7 Ma may have contributed to the ability to tolerate a wider range of landscapes and climates. There is archaeological evidence that hominids had occupied Europe and the Near East by just less than one million years ago, and perhaps as early as 1.6 Ma, and at the southern African site of Swartkrans there is evidence of an 'early *Homo*'-like hominid at ≈ 1.5 Ma. Remains of *H. erectus* persist in the Far East, at the Chinese site of Zhoukoudian (formerly Choukoutien) near to Beijing, as late as 200 Ka. Thus, *H. erectus* remained in at least one region while hominids closer in appearance to modern humans were making their appearance in other parts of the world.

Precursors of modern humans

There is no designated type specimen of *H. sapiens*, and because it is a 'polytypic' species (i.e. it incorporates a relatively large range of variation), a spectrum of skull shapes and limb proportions have to be taken into account when considering whether fossils can be

assigned to *H. sapiens*. However, the variation is not random, and a good deal of it is related to climate. For example, modern human populations follow Allen's Rule which stipulates that populations in warmer climes will have longer extremities, while those in colder climates will have shorter, stockier limbs. Head shape responds in the same way, with long heads linked to warm climates, and round heads and larger noses more common in colder climates. Thus, some of the morphological characteristics of 'anatomically modern' *H. sapiens* differ according to the predominant climate.

However, there are fossils which are more modern human-like than *H. erectus*, yet not fully modern in appearance. Such material is known from Africa (at Ndutu and Kabwe, for example), Europe (at Mauer and Arago), and China (at Dali and Jinnuishan). Perhaps the best-known material in this 'archaic *Homo*' category are the remains which have been attributed to *Homo neanderthalensis* (see Section 1.5.6). This species has a characteristic appearance which includes a large, globular-shaped cranium, jaws and teeth which are set well forward in the face, particularly robust limb bones with large joint surfaces, and DNA that is distinct from modern *H. sapiens* (Krings *et al.* 1997). There is soundly dated fossil evidence for specialized Neandertals by ≈ 125 Ka, and fossil evidence from sites in France and Germany (Biache and Ehringsdorf) may confirm the presence of Neandertals as early as 200 Ka. However, some of these Neandertal specializations can be seen in fossils from the Spanish site of Sima de los Huesos that date from ≈ 300–400 Ka, and researchers have even suggested that Neandertal-like morphology can be detected in the collection of fossils from the Gran Dolina, also in Spain, that dates from ≈ 700–800 Ka. The geologically most recent Neandertals are dated to ≈ 27 Ka.

Neandertals are confined to Western Europe, the Near East, and adjacent parts of Asia. For much of this period the climate in Europe oscillated between cold, glacial phases and shorter, warmer, interglacial periods. The short stature and robust limb bones of the Neandertals are the body shape predicted in colder regions by Allen's Rule.

Populations of 'archaic *H. sapiens*' peoples from other regions are not so characteristic in their appearance, but all have some distinguishing features. The ones from Europe, and adjacent areas, have been assigned to their own species, *Homo heidelbergensis* (Rightmire 1998). There is less of a consensus about the taxonomy of the archaic *Homo* remains from Africa. It is the extent to which regional characteristics persisted in modern populations that lies at the root of debates about the origin of anatomically modern humans.

Modern human origins

There are two competing hypotheses for the origins of modern humans. One, the 'out of Africa' or 'Noah's Ark' hypothesis, suggests that the genetic modifications that were responsible for the shift from an archaic to an anatomically modern morphology occurred only once, and in Africa. The rival 'multiregional' hypothesis proposes that the shift to an anatomically modern human morphology occurred several times, but only once in each region. A modification of these main hypotheses allows for gene flow between the regions, but maintains that it was not sufficient to obscure regionally distinctive morphologies (Brauer 1992).

Evidence about modern human origins comes from the fossil record, and the pattern of modern human variation. The 'out of Africa' hypothesis predicts that adaptively neutral variation in the genotype would be greatest in Africa, where modern human populations have existed for the longest time. Analysis of the variation in mitochondrial DNA, the Y chromosome, and in other systems suggests that this is the case. However, there are explanations other than the antiquity of the regional gene pool, such as drastic reductions in population size and geographical restrictions on the exchange of genes between Africa and the rest of the world, for these results.

The earliest fossil evidence of hominids with a skull, jaws, teeth, and limb bones equivalent to those of contemporary humans comes from Africa. Remains from Klasies River Mouth, southern Africa, from the Omo in Ethiopia, from Lake Turkana in Kenya, and from the Skhul and Qafzeh caves in the Near East all date to ≈ 100 Ka and earlier. However, while this evidence is consistent with the 'out of Africa' hypothesis, it does not 'prove' it. Some regions do not have fossils of this antiquity so that their 'modernity', or lack of it, cannot be judged. The old adage 'absence of evidence is not evidence of absence' means that, while the case for an African origin for early modern humans is a strong one, it is as yet unproven.

Peopling the planet

Anatomically modern humans were dispersed across the Old World by 25–35 Ka. By that time, and perhaps as early as 50–60 Ka, they had also managed to cross from the Asian mainland to Australasia. Reductions in sea level during times of maximum glaciation would have shortened any sea crossings, but the colonizers of Australia must have been able to make a raft, or its equivalent. Archaeological evidence suggests that the occupation of the New World did not take place until 10–12 Ka. Modern humans could have entered the New World across the land bridge that was established

between Siberia and Alaska around 70–20 Ka, but the earliest archaeological evidence of modern human occupation of Siberia dates from just 20–30 Ka. A provocative recent theory suggests that at least one early (≈ 10–12 Ka) ingress of modern humans may have been via the Atlantic to the Eastern seaboard. This suggests that despite the presence of the land bridge, the inclement climate of the latest ice age deterred potential migrants until the climate warmed around 15–13 Ka. Thus by ≈ 13 Ka all the major land masses, except Antarctica, had been populated by *Homo sapiens*.

References

Asfaw, B., White, T., Lovejoy, O., Latimer, B., Simpson, S. and Suwa, G. (1999) *Australopithecus garhi*: a new species of early hominid from Ethiopia. *Science* **284**, 629–635.

Brauer, G. (1992) Africa's place in the evolution of *Homo sapiens*. In: G. Brauer and F.H. Smith, eds. *Continuity and replacement: controversies in* Homo sapiens *evolution*, pp. 83–98. Balkema, Rotterdam.

Brown, F.H., Harris, J., Leakey, R. and Walker, A. (1985) Early *Homo erectus* skeleton from West Lake Turkana, Kenya. *Nature* **316**, 788–792.

Krings, M., Stone, A., Schmitz, R.W., Krainitzki, H., Stoneking, M. and Pääbo, S. (1997) Neanderthal DNA sequences and the origin of modern humans. *Cell* **90**, 19–30.

Partridge, T.C., Bond, G.C., Hartnady, C.J.H., de Menocal, P.B. and Ruddiman, W.F. (1995) Climate effects of late Neogene tectonism and volcanism. In: E.S. Vrba, G.H. Denton, T.C. Partridge and L.H. Burckle, eds. *Paleoclimate and evolution*, pp. 8–23. Yale University Press, New Haven.

Rightmire, G.P. (1998) Human evolution in the Middle Pleistocene: the role of *Homo heidelbergensis*. *Evolutionary Anthropology* **6**, 218–227.

Ruvolo, M. (1997) Genetic diversity in hominoid primates. *Annual Review of Anthropology* **26**, 515–540.

Swisher, C.C., Curtis, G.H., Jacob, T., Getty, A.G., Suprijo, A. and Widiasmoro. (1994) Age of the earliest known hominids in Java, Indonesia. *Science* **263**, 1118–1121.

White, T.D., Suwa, G. and Asfaw, B. (1994) *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature* **371**, 306–312.

Wood, B.A. (1991) *Koobi Fora Research Project*, Vol. 4. *Hominid cranial remains*. Clarendon Press, Oxford.

Wood, B.A. (1992) Origin and evolution of the genus *Homo*. *Nature* **355**, 783–790.

Wood, B.A. and Collard, M. (1999) The human genus. *Science* **284**, 65–71.

1.5.6 Neandertals

L.C. AIELLO

Introduction

The Neandertals are arguably the best-known members of the human evolutionary tree. There are a number of reasons for this. They were the first hominids to bury their dead; burial protects remains from scavengers and the Neandertals are among the first of the early human ancestors for whom relatively good samples of articulated skeletons from individuals of all ages are known. Secondly, Neandertals lived quite recently in time; they first appeared as a species distinct from earlier ancestors at about 125 Ka and did not disappear from the fossil record until ≈ 27 Ka. They also occupied Europe and adjacent areas of Eurasia; as a result, their remains were the first to be found and recognized as human ancestors by European scientists who had been stimulated by the Darwinian revolution in the second half of the nineteenth century.

Who were the Neandertals?

The first two Neandertals found (Engis, Belgium 1829; Gibraltar 1848) remained unrecognized as early humans until after the discovery of the well-known Neandertal skeleton in the Neander Valley (Germany 1856). These early finds were followed by others at La Naulette (1866) and Spy (1886), both in Belgium, and a plethora of material from the Dordogne region of southern France (e.g. La Chapelle-aux-Saint 1908; La Ferrassie 1909–10; La Quina 1908–20; Le Moustier 1908, 1914). Throughout this time, Neandertals were characterized as brutish, with a stooped posture and habitually bent knees.

Neandertals are now known to be much more modern in their body form and behaviour than was first appreciated. The bodies of Neandertals were short, stocky, and robust and have their closest analogue among living peoples such as the Inuit who are physically adapted to living under arctic conditions. Like these living peoples, the Neandertals had relatively short distal extremities (lower legs and lower arms) and relatively wide bodies that serve to maximize internal body volume in relation to surface area, and therefore conserve body heat. This cold-adapted body form may have evolved during Oxygen Isotope Stage 6, the long period traditionally known as the Riss Glaciation (≈186–128 Ka). Probable ancestors of the Neandertals living in Europe, such as Boxgrove (England, 500 Ka) and Sima de los Huesos (Atapuerca, Spain, ≈ 300 Ka), were bigger, although still very robust people (Stringer *et al*. 1998).

Neandertals were not just modern humans adapted to a cold climate. They had wider bodies than today's cold-adapted people and weighed 10% or so more than modern people of equivalent stature. Consistent with their wide bodies were very wide and robust pelves, with unusually shaped, long, and narrow superior pubic rami (bones that form the front of the pelvis). They also had long collar bones, unusually proportioned fingers and toes, extremely robust extremities, and scapulae with details that indicate upper arm strength and shoulder stability. This must reflect adaptively important differences to modern humans in mobility, upper limb loading intensity, and behavioural patterns. Neandertals also had unusually thick cortical bone throughout the skeleton, but particularly in their arms.

The craniofacial skeletons of Neandertals were also unique (Fig. 1.5.6.1). Their faces were very large, with cavernous noses and eye orbits. They had a marked degree of midfacial prognathism, with an associated swept-back, streamlined cheek morphology, a long and relatively flat cranial base, and an elongated foramen magnum. The rear of the skull protruded in an occipital bun. They had large brain sizes that, in absolute terms, exceed the average of modern humans. In relation to inferred body mass, however, their relative brain sizes were marginally lower than those found in modern humans (Ruff *et al*. 1997).

Neandertal adaptation

Some of the Neandertal morphology may have been a direct consequence of living in cold conditions (Churchill 1998). One hypothesis suggests that their short and squat bodies were the result of an endocrine shift during ontogeny, where heightened levels of androgens promoted rapid somatic growth, muscle development, and early closure of the epiphyses (termination of long bone growth), resulting in a short and stocky body. High levels of androgens could also be related to general bone thickness, browridge, nasal, alveolar, and sinus development, and molar taurdontism (a characteristic expansion of the pulp cavities in the molar teeth). Selection may also have favoured large and robust babies, able to withstand the relatively cold conditions. Accelerated growth in the cartilaginous precursors of bone, particularly in the cranial base, during late fetal development could have contributed to the unusual cranial morphology of Neandertals (Smith 1991). This accelerated development is also consistent with other evidence suggesting that dental and brain development was marginally more rapid in Neandertals than in modern European children (Stringer *et al*. 1990).

Other early hominids share some of the robusticity of Neandertals, suggesting that at least some unique features of Neandertal morphology may have more complicated causes than a simple endocrine adjustment to cold weather conditions. Neandertal upper limb robusticity, as well as features such as the orientation of their joints, might reflect the need for strength and endurance under difficult foraging circumstances. This is consistent with the fact that the Mousterian tool industry, with which the majority of the Neandertals are associated, implies: (1) close-contact hunting using short-range weapons; and (2) high reaction forces in the upper limb during, for example, flint knapping, woodworking, and other subsistence activities.

There is considerable evidence for a difficult and strenuous Neandertal life. Age at death suggests not only a high level of mortality at all ages but also a particularly high level of mortality among young adults. There

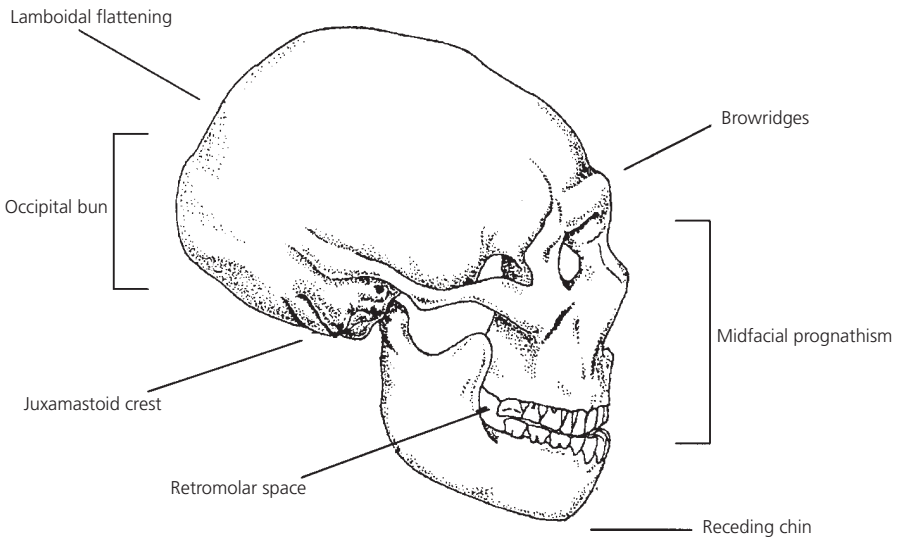

Fig. 1.5.6.1 Reconstruction of Neandertal skull from Shanidar, Iraq, illustrating some characteristic cranial features.

are high levels of enamel hypoplasia (malformation of dental enamel) that seem to indicate particular stress around the time of weaning. The great majority of adult Neandertal skeletons also show indications of trauma and/or infection.

Neandertal cognitive abilities

There is debate over the cognitive abilities of the Neandertals. Some archaeologists suggest that Neandertals lacked concern for the visual appearance of the tools they made. This is because the Mousterian tools seem to grade into one another without clear-cut typological divisions (Mellars 1998). This lack of patterning in the stone tools might suggest that Neandertals lacked a highly structured vocabulary for the different artefact types. The absence of complexity in many aspects of Neandertal culture also suggests that they may have had limited capacity to organize and structure their activities. This contrasts with the Upper Palaeolithic cultures of anatomically modern humans who entered Europe ≈ 40 Ka. The greater degree of both chronological and spatial variation in technology associated with these modern humans suggests that they might also have had more sharply defined ethnic divisions. This contrast between the Neandertal Mousterian culture and the modern human Upper Palaeolithic cultures may also reflect fundamental linguistic differences; language is used to transmit tightly defined rules of complex behaviour and is a catalyst to the emergence of sharply defined cultural traditions.

The suggestion that the Neandertals may not have had a system of vocal communication characterized by any or all of the symbolic and syntactic features which define modern human language is surprising in the context of other evidence. Neandertals had large and energetically expensive brains and also would have had a vocal apparatus entirely compatible with the production of the full range of human speech sounds (Aiello 1998). Toward the end of their known existence (≈30–36 Ka), Neandertals in France are found with the more advanced Chatelperronian culture (at Arcy-sur-Cure and St Cesaire) characterized by simple bone tools, red ochre, perforated animal teeth, and other forms of personal decoration, in addition to more elaborate stone tools. These cultural aspects are otherwise associated only with anatomically modern humans. It is a matter of debate whether the Neandertals copied these traits from contemporary modern human populations or invented them independently as these populations were entering and dispersing across Europe (d'Errico *et al.* 1998).

This is all the more interesting because the last surviving Neandertals apparently occupied the Iberian peninsula south of the Ebro river for at least 5000–10 000 years after the arrival of modern populations in the adjacent parts of northern Spain and the Mediterranean coast, at ≈ 40 Ka. These isolated, remnant Neandertal populations show no indication of the more elaborate cultural elements found in the Chatelperronian sites further north.

The apparent difference between the archaeological remains of Neandertals and anatomically modern humans, and the complexities surrounding their inferred linguistic and cognitive abilities, are particularly relevant in the context of mitochondrial DNA evidence (Krings *et al.* 1997). This suggests that Neandertals are genetically distinct from all modern humans and that the two lineages had separate evolutionary histories for about 500 kyr. This would have been sufficient time to allow different cognitive processes, possibly including language, to develop in both lineages.

The question of differences in Neandertal cognitive abilities remains unanswered. The best evidence to date suggests that modern humans had arrived in the Near East by ≈ 100 Ka but penetrated no further north or west at this time. Like the Neandertals, these early modern people used Mousterian tools and may simply not have had the behavioural sophistication to compete with the Neandertals, who were biologically adapted to the ice-age conditions of Europe. In fact, these early moderns disappear from the Near East ≈ 80 Ka, leaving Neandertals as the sole occupants of the area until the moderns return ≈ 40 Ka with their more sophisticated Upper Palaeolithic tool culture. Whether the evolution of Upper Palaeolithic cultures implied significant advances in cognitive evolution amongst these modern humans relative to the Neandertals has not been established. The Chatelperronian culture suggests that Neandertals had the necessary cognitive capability to make and use more elaborate tools and symbolic artefacts. If so, the evolution of the Upper Palaeolithic may have had more to do with the social and/or environmental pressures on early modern humans than with any major cognitive differences between them and the Neandertals.

Conclusion

Neandertals are best interpreted as an extinct subspecies of archaic *Homo sapiens* which had been largely isolated from mainstream human evolution in Africa and Asia for at least the latter half of the Middle Pleistocene and the early part of the Upper Pleistocene. They were biologically well adapted to the glacial conditions of northern Europe, but there is also evidence that their life was hard. Modern humans arrived in Europe with their more sophisticated Upper Palaeolithic culture at ≈ 40 Ka when the climate was deteriorating towards the last glacial maximum. In the context of deteriorating environmental

conditions, competition with the better equipped early moderns could only have put increasing pressure on the Neandertals, pushing them into more peripheral environments, increasing their levels of mortality, and ultimately driving them to extinction.

References

Aiello, L.C. (1998) The foundations of human language. In: N. Jablonski and L.C. Aiello, eds. *The origin and diversification of language*, pp. 21–34. Memoirs of the California Academy of Sciences, No. 24. University of California Press, San Francisco.

Churchill, S.E. (1998) Cold adaptation, heterochrony, and Neandertals. *Evolutionary Anthropology* **7**, 46–61.

d'Errico, F., Zilhao, J., Julien, M., Baffier, D. and Pelegrin, J. (1998) Neanderthal acculturation in western Europe? A critical review of the evidence and its interpretation. *Current Anthropology* **39**, S1–S44.

Krings, M., Stone, A., Schmitz, R.W., Krainitzki, H., Stoneking, M. and Pääbo, S. (1997) Neandertal DNA sequences and the origin of modern humans. *Cell* **90**, 19–30.

Mellars, P. (1998) Neanderthals, modern humans and the archaeological evidence for language. In: N. Jablonski and L.C. Aiello, eds. *The origin and diversification of language*, pp. 89–116. Memoirs of the California Academy of Sciences, No. 24. University of California Press, San Francisco.

Ruff, C.B., Trinkaus, E. and Holliday, T.W. (1997) Body mass and encephalization in Pleistocene *Homo*. *Nature* **387**, 173–176.

Smith, F.H. (1991) The Neandertals: evolutionary dead ends or ancestors of modern people? *Journal of Anthropological Research* **47**, 219–238.

Stringer, C.B., Dean, M.C. and Martin, R.D. (1990) A comparative study of cranial and dental development within a recent British sample and among Neandertals. In: C.J. De Rousseau, ed. *Primate life history and evolution*, pp. 115–152. Wiley-Liss, New York.

Stringer, C.B., Trinkaus, E., Roberts, M.B., Parfitt, S.A. and Macphail, R.I. (1998) The Middle Pleistocene human tibia from Boxgrove. *Journal of Human Evolution* **34**, 509–547.

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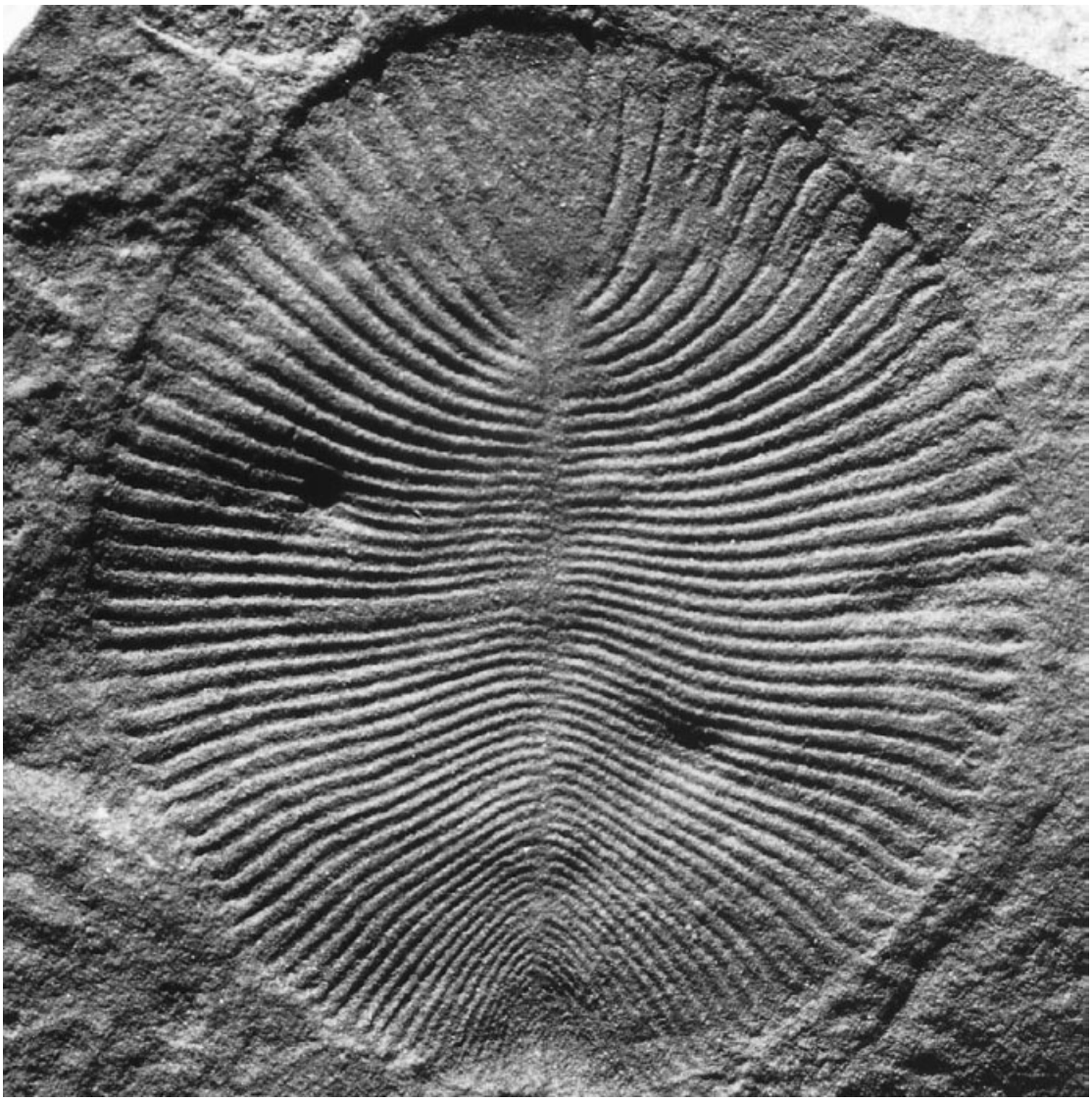
2
THE EVOLUTIONARY PROCESS AND THE FOSSIL RECORD



The Precambrian metazoan *Dickinsonia costata* from the late Proterozoic Ediacaran interval, Flinders Ranges, South Australia, ×1.6. (Photographed by D.E.G. Briggs at the University of Adelaide.)

2.1 Species Evolution

2.1.1 Speciation and Morphological Change

D.B. LAZARUS

Introduction

The words 'species' and 'speciation' are frequently used in different ways by different scientists. Species are, in the sense of this article, groups of individuals which exchange genetic information primarily with other members of the group, and which share a common evolutionary history. This 'evolutionary species' definition derives from G.G. Simpson, and corresponds to the palaeontological term 'lineage'. It includes, but is not limited to, non-time-dimensional concepts of species such as the biological species concept, and species concepts for organisms that reproduce, at least in part, by asexual means. Species can change through time within a lineage without dividing: this process is called phyletic evolution, or 'anagenesis'. If change is substantial, the lineage may be divided by taxonomists into different taxonomic species. Speciation, however, as used here is the creation of a new lineage, separate from the ancestor species, typically by the splitting or 'cladogenesis' of one lineage into two or more descendants. Speciation is the more important of these two biological processes, increasing biological diversity and creating new units upon which evolution can act.

In living populations, species boundaries can sometimes be determined by breeding experiments, although in practice most species are defined by the clustering of individuals measured by morphological or other characters. Fossil species are normally defined by this morphological clustering criterion, with reference when possible to living representatives for determining scales typical of between-species differences.

Studies, lasting a few years or so, of adaptation and change in laboratory populations of test organisms (e.g. the fruit fly *Drosophila*) have demonstrated that limited amounts of morphological change can occur in populations quite rapidly. However, in the real world, the much larger amounts of evolutionary change required for speciation typically occur over much longer periods of time, not directly observable by scientists. Most of our ideas about speciation come, none the less, from studying the results of speciation as displayed in living organisms, and inferring the mechanisms responsible. These results include the distribution of individuals, characters, and genes along environmental geography, and the patterns of gene flow within and between populations. Studying the temporal unfolding of speciation events from time series of fossils is, in important ways, a more direct method of investigation, and is the only method that can examine phyletic change. Due to the sporadic nature of most fossil records, however, such studies have been less used.

Biological studies of speciation

Biologists have produced several models of speciation processes (Bush 1975). Geographically based models assign a major role to the physical isolation of populations, which diverge into new species as a result. The isolated populations can be large, or, in the widely known 'peripheral isolate' model, small and typically located near the margin of the geographical range of the ancestral species. Ecological models stress the role of differential ecological adaptation in creating species divergence, even without geographical isolation. The 'parapatric' model of speciation along continuous ecological gradients is one example. Genetic models stress the role of 'internal' genetic mechanisms in creating new taxa. Examples include polyploidy (changes in basic chromosome number) and hybridization (the mixing of genomes from two or more ancestral taxa to create a new species). These models have been particularly well developed in botany (Grant 1971).

Biological research in recent years has established the probable existence of all these mechanisms, but has not been able to determine their relative importance in the evolution of life. One basic problem is that, in most cases, the observed characteristics of living species can be ascribed to more than one model of speciation. For example, two sister species occupying geographically adjacent areas could have evolved initially by geographical isolation, with only secondary re-establishment of contact, or without any period of isolation—evolving instead by divergence and disruption of a regular, geographically continuous gradient of differentially adapted local populations (a 'cline'). Frequently only the time history of the origin of a species can reveal which evolutionary path was followed, and obtaining this temporal record requires palaeontological data.

Palaeontological studies of speciation

Palaeontological studies of species-level evolution have been available for many decades. Older studies frequently described morphological change within a lineage as observed in a single stratigraphic section—data that speak to phyletic evolution, rather than speciation. Such patterns of change, often quite gradual, have been reported for mammals, echinoderms, brachiopods, and many groups of microfossils (e.g. Fig. 2.1.1.1). In such studies, change equivalent to that which separates sister species typically is shown to accumulate over a period of several hundred thousand to several million years. Many taxa, however, do not show any significant change over similar periods of time—a phenomenon called morphological stasis.

Studies that examine speciation (e.g. lineage splitting) are less common, and have yielded a variety of results. Mollusc data have been used to infer gradual rates of branching (Geary *in* Erwin and Anstey 1995), a pattern documented in more detail in several studies of microfossils (radiolarians, diatoms, and planktic foraminifera, e.g. papers in Berggren and Casey 1983; Lazarus 1986; Lazarus *et al*. 1995) (Figs 2.1.1.2 and 2.1.1.3). These studies record ancestral, transitional, and descendant forms within the same sediments, suggesting that geographical separation was not the primary factor causing speciation. Other studies (molluscs in lakes, bryozoans, trilobites) have revealed a pattern of abrupt 'punctuated' appearance of new species from putative ancestors, with a lack of transitional forms suggesting that speciation events occurred elsewhere, and were not preserved in the sedimentary records studied (Cheetham 1986; Cheetham and Jackson *in* Erwin and Anstey 1995) (see Section 2.1.2).

Lastly, a variety of indirect methods have been proposed to evaluate speciation mechanisms, such as statistically comparing measured rates of phyletic evolution with the inferred duration of speciation events to determine whether rate differentials (and thus different possible causal mechanisms) exist between these types of evolutionary change; or using phylogenetic trees to estimate the relative frequencies of phyletic evolution and speciation within a clade (Stanley 1979; Wagner and Erwin *in* Erwin and Anstey 1995).

Problems and limitations of current knowledge

There are many lower-level taxonomic, stratigraphic, and biogeographical hypotheses upon which palaeontological studies of speciation are based, and confirming their validity has often been very difficult. The specimens being studied must indeed belong to a single lineage or set of sister lineages, and all branches of such a clade of sister taxa must be included in the study. Micropalaeontological studies in particular have not always paid sufficient attention to these taxonomic prerequisites. The relative geochronological age of samples must be established accurately, and the possible effects of the migration of morphologically variable geographical populations (e.g. clines) must be controlled. Many of the published studies of invertebrates and vertebrates are potentially vulnerable to such problems. The evolutionary significance of the morphological changes observed must be determinable, a particular problem in some studies (e.g. fossils from lake sediments) where only very short lived fluctuations in the morphology of populations are seen. Indirect taxic methods depend on many simplifying assumptions about the nature of fossil species data and speciation mechanisms, and ignore numerous other factors, such as migration and ecolo-

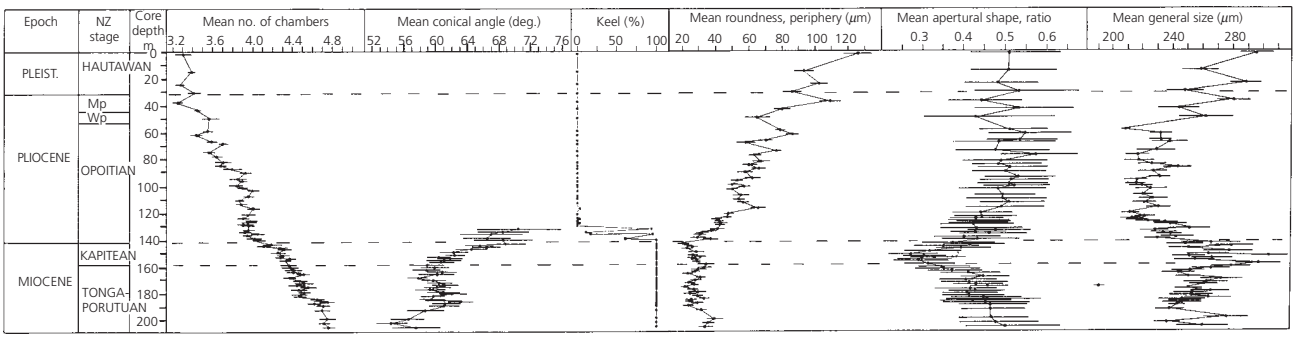


Fig. 2.1.1.1 Example of gradual phyletic evolution within a single planktic foraminiferal lineage (*Globorotalia conoidea–G. inflata*). Plotted: means and 95% confidence intervals of morphological characters of sample populations from South Pacific DSDP Site 284. New Zealand Stage abbreviations: Wp, Waipipian, Mp, Mangapanian. This morphological series is recognized and used biostratigraphically throughout the temperate regions of the world, and the lineage is divided for biostratigraphic purposes into four different species. Morphological evolution for many key taxonomic characters is quite gradual and fairly uniform in rate over a period of more than 8 myr. (From Malmgren and Kennett 1981.)

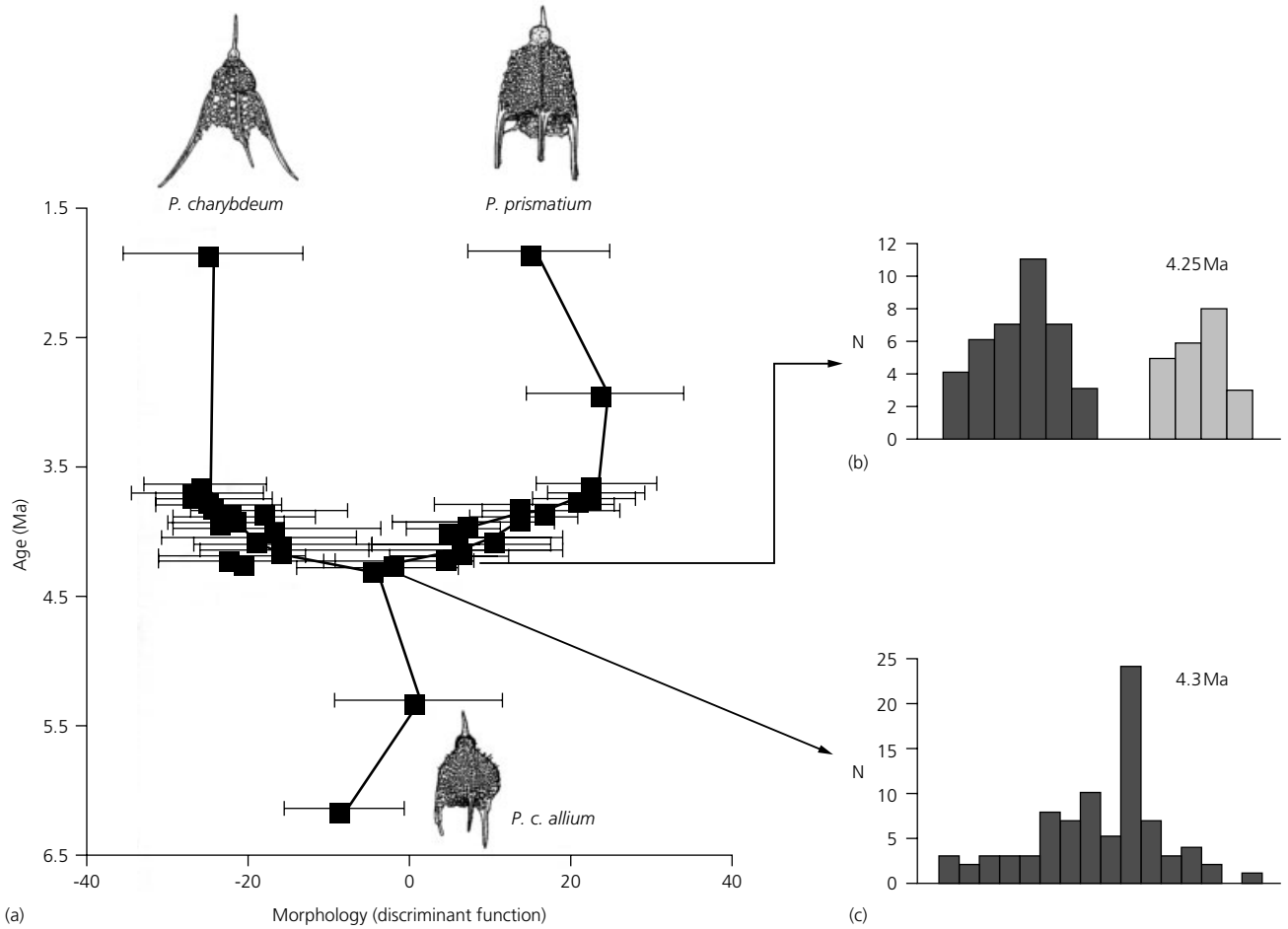


Fig. 2.1.1.2 Speciation and phyletic evolution in the Pliocene radiolarian lineages *Pterocanium charybdeum* and *P. prismatium*. Measured morphological characteristics for several thousand individuals were scored by discriminant functions. *Pterocanium prismatium* evolves from a subspecies of *P. charybdeum* (*P. c. allium*) at ≈ 4.3 Ma. (a) Population means (connected by vertical lines) and population standard deviations (horizontal lines) for a series of samples taken from equatorial Pacific DSDP Site 573. (b,c) Histograms of discriminant scores for two samples from the base of the speciation event show initial break-up of the population within an estimated 50-kyr interval. Data from younger samples, however, show that an even larger amount of morphological change accumulated in the next 500 kyr by phyletic evolution in both descendant lineages before coming to a stop: net change after this time interval was near zero. (Redrawn from Lazarus 1986.)

gically controlled local variations that can affect species stratigraphic ranges. Lastly, most studies make use of various complex morphometric and statistical methods which can introduce unrecognized distortions into the analysis. Despite these problems, some tentative conclusions can be drawn from the research carried out to date.

Conclusions and prospects

It is now well established that speciation and phyletic evolution can sometimes be recognized in the fossil record, and that such palaeontological data can provide highly useful tests of speciation theories.

Widespread phyletic evolution, gradual transitions between species, and the presence of both the ancestral and descendant lineages in the same sedimentary sequence in groups such as marine microplankton argue strongly against any geographical isolate model of speciation. Ecological or genetically driven speciation mechanisms must be responsible in these cases.

Equally, the preponderance of morphological stasis and the punctuated appearance of new species in some other groups of organisms (e.g. many invertebrates) suggest that here the peripheral isolate model of speciation is at work. Thus, there is limited support in the fossil record for the theory of 'punctuated equilibrium', although only for some taxa. This theory—derived from the peripheral isolate speciation model's predictions of

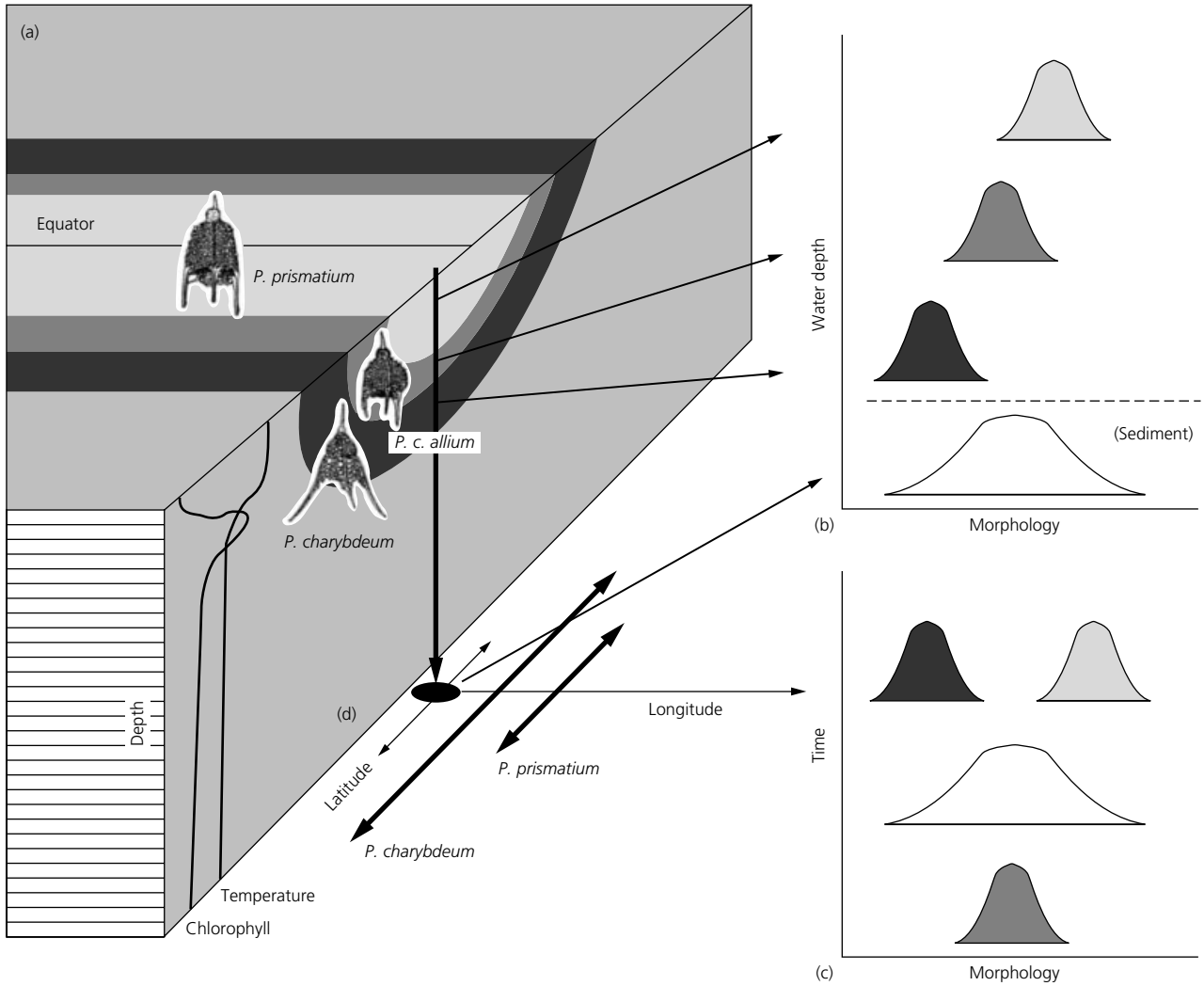


Fig. 2.1.1.3 Model for the evolution of *Pterocanium*. (a) New, surface-water (light tint) tropical species *P. prismatium* evolves from tropical, intermediate-water ancestral species *P. charybdeum allium* via disruption of a water-depth distributed cline (ancestor living in intermediate environments shown by dark tint). Water depth in planktic environments correlates strongly to gradients in biologically important parameters, e.g. temperature and nutrients (curves in lower corner of (a)). (b) Living water-column populations of cline, relative to water depth; lower curve shows combined distribution as recorded in the sediment record below (cumulative rain of shells to sediment shown by vertical black arrow in (a)). (c) Temporal record in the sediments of speciation is marked by loss of intermediate populations in the cline (central part of medium tinted distribution) and phyletic evolution in both descendant lineages; compare Fig. 2.1.1.2. (d) The geographical predictions of this model (double headed arrows show latitudinal range of taxa), i.e. a tropical distribution for *P. prismatium*, and a broader subtropical distribution for descendant populations of *P. charybdeum*, are observed in the fossil record.

stasis within species and rapid rates of change during speciation—has important implications for understanding macroevolutionary change (see Section 2.3).

These initial conclusions represent only a fraction of what may still be possible. Speciation by hybridization, for example, makes highly testable predictions of pattern for fossil records, and may be common in many groups of organisms, such as plants and protists. To date, there have been almost no palaeontological studies of this potentially important evolutionary mechanism.

Palaeontological speciation studies may play a role in addition to the specific goal of testing speciation theories. The field of evolutionary research is highly fragmented, with subdisciplines working on materials, and thus mechanisms, that occur at very different observational scales. This is particularly true of biological and palaeontological evolutionists. A broader palaeontological research effort on species evolution could be used to demonstrate how lower-level processes, determined at neontological scales, influence larger-scale patterns of

macroevolutionary change, and could thus contribute significantly to a more unified understanding of biological evolution. The theories that comprised 'punctuated equilibrium' represented one of the most ambitious, if ultimately not entirely successful, recent efforts to reunite these two branches of evolutionary science. It is no coincidence that the core of punctuated equilibrium theory is based on palaeontological studies of speciation. The challenge for the future is to use speciation studies more effectively to build bridges between these two fields.

References

Berggren, W.A. and Casey, R.E., eds. (1983) Symposium on tempo and mode of evolution from micropaleontological data. *Paleobiology* **9**, 326–428.

Bush, G.L. (1975) Modes of animal speciation. *Annual Review of Ecology and Systematics* **6**, 339–364.

Cheetham, A.H. (1986) Tempo of evolution in a Neogene bryozoan: rates of morphologic change within and across species boundaries. *Paleobiology* **12**, 190–202.

Erwin, D.H. and Anstey, R.L., eds. (1995) *New approaches to speciation in the fossil record*. Columbia University Press, New York.

Grant, V. (1971) *Plant speciation*. Columbia University Press, New York.

Lazarus, D.B. (1986) Tempo and mode of morphologic evolution near the origin of the radiolarian lineage *Pterocanium prismatium*. *Paleobiology* **12**, 175–189.

Lazarus, D.B., Hilbrecht, H. and Spencer-Cervato, C. (1995) Speciation and phyletic change in *Globorotalia truncatulinoides* (planktonic foraminifera). *Paleobiology* **21**, 28–51.

Malmgren, B.A. and Kennett, J.P. (1981) Phyletic gradualism in a late Cenozoic planktonic foraminiferal lineage; DSDP Site 284, southwest Pacific. *Paleobiology* **7**, 230–240.

Stanley, S.M. (1979) *Macroevolution: pattern and process*. W.H. Freeman, San Francisco.

2.1.2 Evolutionary Stasis vs. Change

A.H. CHEETHAM

Introduction

'*. . . stasis is data . . . each case of stasis has as much meaning for evolutionary theory as each example of change*.' (Gould and Eldredge 1977, p. 116)

'*This is . . . the issue of stasis, which I believe to be the legitimate problem spawned by the punctuated equilibrium model*.' (Levinton 1988, p. 379)

Thus do the proponents of the punctuated equilibria model and one of its chief critics agree about the central role of stasis in the ongoing debate over evolutionary tempo and mode. If species are generally static in morphology, the evolutionary change necessary to account for the taxonomic and morphological diversity of the fossil record must be concentrated in the geologically brief intervals during which species originate. In the punctuated equilibria model, recognition of the episodes of change is constrained by our ability to resolve the temporal differences between successively sampled populations. Sampling resolution varies with rates of sediment accumulation, but is ordinarily no better than tens of thousands to hundreds of thousands of years. In the view of population geneticists, such a time scale is still protracted enough to allow standard neo-Darwinian mechanisms to explain species' origins.

The punctuated equilibria model explicitly relates the episodes of change to lineage splitting (cladogenesis), the process to which the term 'speciation' is now generally understood to apply (see Section 2.1.1). Indeed, Mayr (1992) regards punctuated equilibria, except for the pervasiveness of stasis, to be equivalent to the model of peripatric speciation (in small, geographically isolated, founder populations) that has been widely accepted since he proposed it in 1954. Stasis, however, is not peculiar to evolutionary patterns involving cladogenesis. Patterns of stasis punctuated by abrupt change have also been found within lineages (punctuated anagenesis; see Jackson and Cheetham 1999). On the other hand, patterns in which morphologically static ancestor species continue to exist along with their static descendants are recognizably consistent with the punctuated equilibria model, by what has been termed the persistence criterion (Levinton 1988).

Even considered strictly empirically, stasis can be an elusive concept. Few if any systematists would expect the morphology of a species to remain truly constant in time or in space. Thus, changes within species must be calibrated by comparison with differences among species. Such comparison involves both the magnitude of change and its directionality, i.e. whether intraspecific change is cumulative or 'cancels out'. Moreover, changes in morphological characters can be directional and still irrelevant to the differences between a species and its nearest relatives, either morphologically or temporally. Therefore, in any given case, evolutionary stasis may be different from character stasis (Levinton 1988), and inevitably the separation of stasis and change requires a hypothesis of phylogenetic relationship among species as its background.

The punctuated equilibria model and its alternative, phyletic gradualism, are more than just descriptions of evolutionary patterns; they are also hypotheses about

the modification of genetic relationships by natural selection and random genetic processes. Regardless of whether a pattern is identified as punctuated or gradual, the magnitude of interspecific differences, and the rates at which such differences emerged, provide the basis for inferences about the relative importance of selection and random change.

Are morphospecies adequate?

In the punctuated equilibria model, a species remains static for virtually all of its duration, typically millions of years, following the comparatively brief interval of change associated with its origin. Thus, stasis is a long-term phenomenon requiring palaeontological data for its identification. Inevitably, the question of whether biological species can be recognized in the fossil record is raised (Levinton 1988). Fossil species are morphospecies, for the most part based on preservable skeletal morphology, and thus could represent suites of morphologically indistinguishable biological species or, conversely, intraspecific ecophenotypic variants. In either case, stasis in morphospecies would have little if any meaning for patterns of speciation.

Genetic studies of living representatives of taxa in which detailed patterns of morphological evolution have been worked out suggest a close correspondence between morphospecies and genetic differences (e.g. Jackson and Cheetham 1994). However, correspondence is maximized only if the smallest statistically significant differences in morphology are used to discriminate species. It is equally important to take into account the possible effects of functional polymorphism, ontogeny, and other sources of intraspecific variation on these morphological differences. Under these conditions, the probability that patterns of morphospecies differentiation through time have evolutionary significance increases greatly.

Tests for stasis vs. change

The identification of evolutionary stasis is fundamentally a statistical question of whether the tempo of change within species is, or more to the point is not, sufficient to account for differences between species. The adequacy of sampling, morphologically as well as spatially and temporally, is thus a major issue. G.G. Simpson recognized as long ago as 1953 the possibility that temporal trends in single characters could be misleading (see Cheetham 1987). He predicted that multivariate statistical methods would eventually be employed routinely in the analysis of overall morphological change. Despite the potential power of the multivariate approach, and the ease with which it can be executed since the advent of personal computers, most studies of intraspecific change have been for single characters (Levinton 1988).

Detailed stratigraphic and geographical sampling is important not only to increase the resolution of observed changes within species, but also to minimize the confidence intervals (i.e. range extensions) for the times (and geographical venues) at which species actually originated. The closer the correspondence between observed first occurrences of species and the confidence limits for their true times of origin, the more useful stratigraphic data become. Most significantly, times of origin are essential for choosing among alternative hypotheses of descent (phylogenetic relationship), and thus for determining the magnitude and direction of interspecific morphological differences against which intraspecific change is to be judged. In addition, for morphology that does show directional change, the timing relative to the time and place of origin of putative descendants becomes important.

Morphological characters measured on a continuous scale (i.e. metric characters) are the most obviously suited to statistical analysis. However, quantitative genetic theory suggests that traits showing discontinuous variation (i.e. meristic or coded qualitative characters) can usually be treated as though continuously varying on a scale with threshold values. Therefore, all characters can potentially be incorporated in a multivariate analysis of intraspecific change with relatively slight risk of serious violation of underlying statistical assumptions. A major advantage of using a standard multivariate statistical approach, such as discriminant function analysis, is that characters invariant within species are automatically eliminated from calculations, thus avoiding an inherent bias in favour of stasis. However, quantitative genetic theory also requires that all traits that do vary be included, because it is assumed not only that each trait is affected by many genes, but also that each gene affects many traits (pleiotropy). Applied to two species of a putative ancestor–descendant pair, discriminant function analysis reduces intraspecific changes in multiple characters to a single track of change. This track lies in the morphological direction that distinguishes the species from each other and thus has direct relevance to the comparison of intraspecific change with interspecific difference.

A series of tests is available for stasis within species, using discriminant scores in place of the changes in single characters employed in earlier studies (Cheetham 1986). The initial assumption (null hypothesis) of these tests is that rates of change within and between species are the same, i.e. that species differentiated gradually. The advantage of this approach is that the identification of stasis requires rejection of the null hypothesis, increasing statistical rigour. If intraspecific change is significantly slower than that between species by this

test, further tests can be made to confirm the interpretation of stasis. Appropriate follow-up tests are whether net intraspecific change is significantly different from zero, and whether a pattern of no net change could conceal sustained directional trends that cancel each other out.

Bryozoans as a model system

Organisms that grow by budding morphologically variable but genetically homogeneous modules (e.g. zooids within bryozoan colonies) offer some special opportunities for the investigation of evolutionary tempo and mode. First, most characters—whether metric, meristic, or coded—behave as continuous variates, because zooids with different states of a character occur in varying proportions from colony to colony (Cheetham 1987). More significantly, breeding experiments with living bryozoan species have shown that the differences between colonies in the mean values for most characters correspond closely to the genetic component of total phenotypic variation (see Cheetham *et al.* 1995). Hence, it is possible to estimate what proportion of the morphological variation in fossil species is heritable, thus blunting criticism that the genetic determinacy of characters is inadequately known (Levinton 1988). Indeed, with relatively few assumptions, it is even possible to reconstruct genetic covariances (or genetic correlations) among characters sufficiently to allow the possible effects of selection and random genetic drift in the differentiation of fossil species to be calculated using standard quantitative genetic methods (see Cheetham *et al.* 1995).

The multivariate tests discussed above revealed remarkably consistent evidence for stasis in the Caribbean Neogene species of the bryozoan *Metrarabdotos* (Figs 2.1.2.1 and 2.1.2.2) (Cheetham 1986). For all nine ancestor–descendant species pairs in which stratigraphic detail was sufficient, the null hypothesis of gradual evolution was rejected at a significance level of at least 0.05, and in almost all cases at 0.001. Confidence intervals for first occurrences of these species are generally short, supporting the inference of

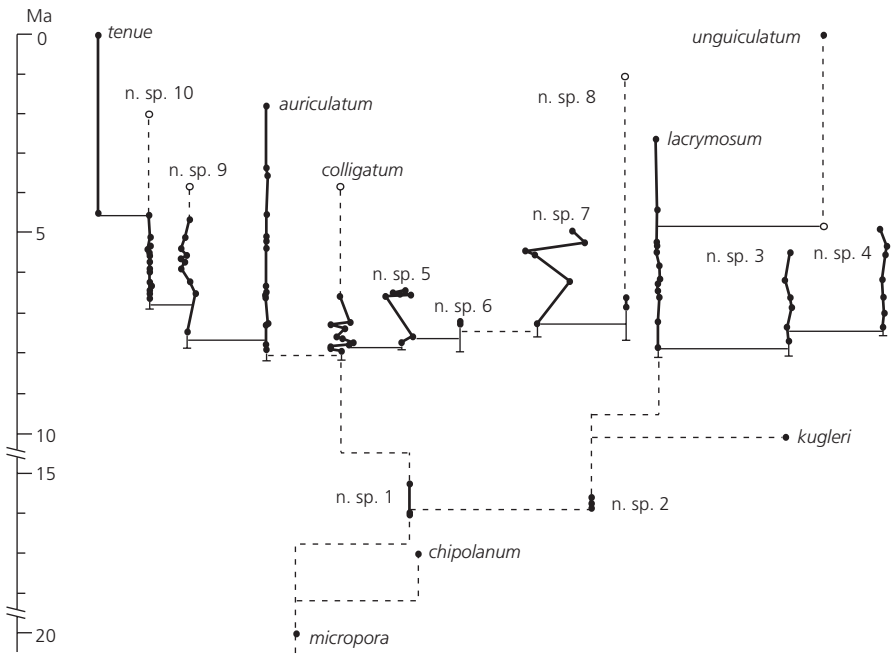


Fig. 2.1.2.1 Changes in overall morphology within and among Caribbean Neogene species of the bryozoan *Metrarabdotos*. All morphological changes are based on discriminant analysis using 46 characters. Each filled circle represents the mean of five zooids from each of one to five colonies from a single stratigraphic level. Open circles represent range extensions made since the original analysis, based on new occurrences reported in work in press. Error bars (95% confidence intervals) have been added for the first occurrences of species represented by material from four or more levels (after Cheetham and Jackson 1995). Ancestor–descendant relationships, inferred by stratigraphic and morphological proximity, are indicated by horizontal lines, the lengths of which are proportional to interspecific differences in overall morphology. Putative ancestor–descendant species pairs connected by solid lines were included in the original analysis of rates of morphological change within and between species; pairs connected by dashed lines are either represented by too few samples for detailed comparison or have unresolved ancestor–descendant polarity. The time scale, in millions of years before the present (Ma), is based on interpolation between biostratigraphic markers (see Cheetham 1986). (Modified from Cheetham 1986.)

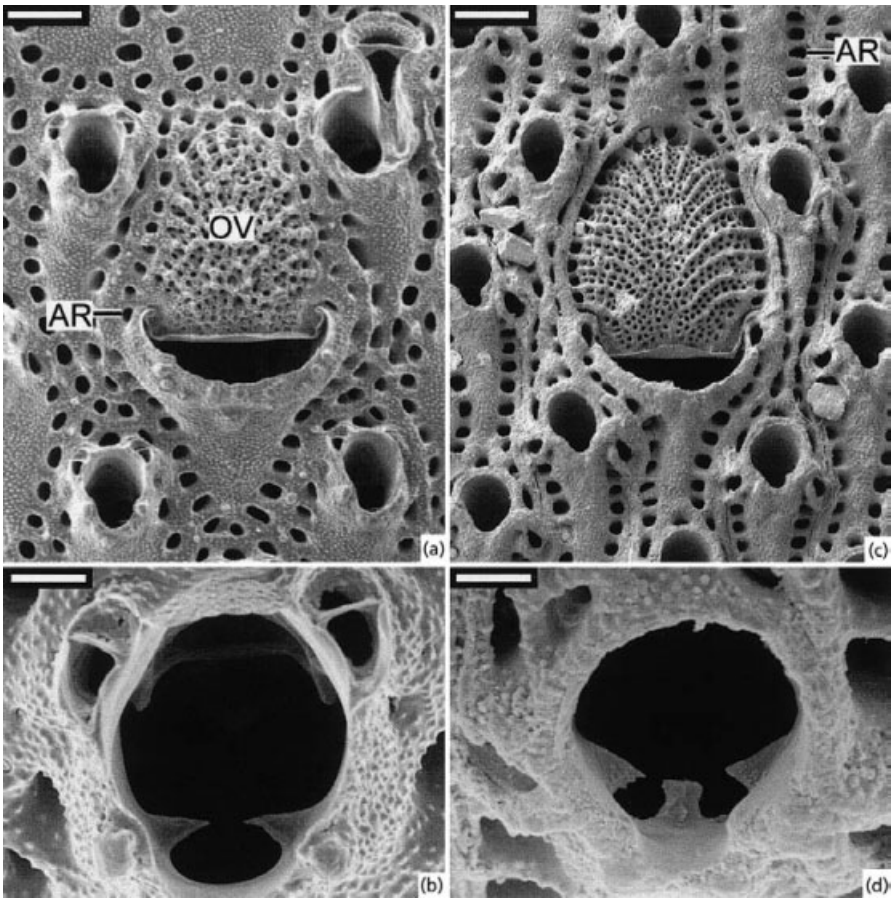


Fig. 2.1.2.2 Morphology of *Metrarabdotos*. (a) *M. tenue* (Busk), Recent, Puerto Rico; AR, proximal areola on the ovicell (OV). (b) Detail of an orifice of *M. tenue* with paired proximal denticles. (c) *M. lacrymosum* Canu and Bassler, Pliocene, Dominican Republic; AR, frontal areola. (d) Detail of an orifice of *M. lacrymosum* with median and paired proximal denticles. Scale bars = 0.25 mm (a,c) or 50 µm (b,d).

ancestor–descendant relationships by stratigraphic proximity and overall morphological similarity (stratophenetics). By minimizing interspecies morphological differences, this approach biases against finding stasis, adding to the rigour of the test. However, any pairing of ancestor with descendant species is only as good as the completeness of the fossil record allows. The completeness with which bryozoan species are represented in the tropical American Neogene was estimated to vary from 70% to more than 90%, with genera such as *Metrarabdotos* at the high end (Cheetham and Jackson *in* Donovan and Paul 1998; based on a method devised by M. Foote and D.M. Raup).

Follow-up tests on the *Metrarabdotos* species provided strong evidence in all cases that intraspecific changes in overall morphology are merely fluctuations around a near zero, otherwise unchanging rate. The consistency of these results is all the more remarkable given the obvious differences from species to species in the magnitudes of both intraspecific fluctuations and interspecific differences (Fig. 2.1.2.1). Moreover, species pairs were found to meet the persistence criterion (survival of the ancestor after giving rise to the descendant), except in two cases (*M.* n. sp. 10–*M. tenue* and *M. lacrymosum*–*M. unguiculatum*), both of which are now known to show persistence (Cheetham *et al*. 1999).

These results were compared with patterns of change in each of the 46 characters (examples shown in Fig. 2.1.2.2) on which the multivariate analysis was based (Cheetham 1987). Some changes (7% of all cases) were found to be correlated with time in all nine of the putative ancestor species, through either part or all of the stratigraphic range of a species, in seeming contradiction to the static pattern in overall morphology. However, only four sets of changes (<1%) are appropriately orientated morphologically and stratigraphically relative to putative descendants (Fig. 2.1.2.3a,b); such changes were found in only three of the nine ancestor species. The rarity of temporally correlated intraspecific change in single characters, together with its weak association with interspecific differences (Fig. 2.1.2.3c,d), suggests chance departure from a general condition of no change within species. Thus, the single-character and multivariate results appear to be reconciled.

Evolutionary significance of stasis and change

Evidence continues to accumulate for the pervasiveness

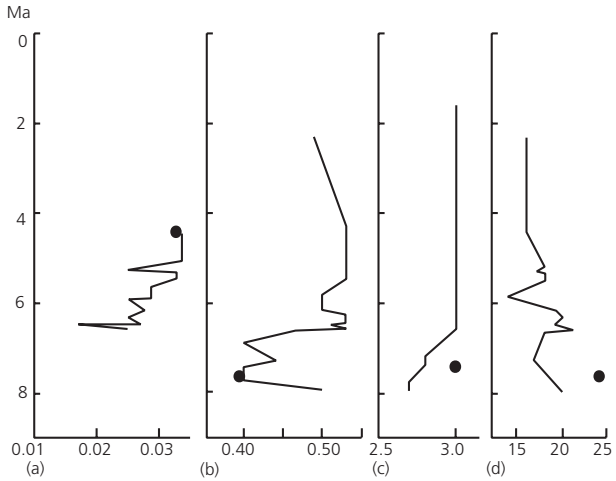


Fig. 2.1.2.3 Examples of changes in single morphological characters in *Metrarabdotos* species. Each line tracks the changes in mean value in the putative ancestor species, and the solid circle represents the mean value in the earliest sample of the presumed descendant. (a) Diameter of proximal areola on ovicell (mm) in *M.* n. sp. 10 relative to *M. tenue* (see Fig. 2.1.2.2a). (b) Ovicell length (mm) in *M. lacrymosum* relative to *M.* n. sp. 3 (see Fig. 2.1.2.2c). (c) Number of oral denticles in *M. auriculatum* relative to *M.* n. sp. 9 (see Fig. 2.1.2.2b). (d) Number of areolae in *M. lacrymosum* relative to *M.* n. sp. 3 (see Fig. 2.1.2.2c). In (a) and (b), statistically significant change in the ancestor is appropriate in time and morphological direction in relation to the value in the descendant. After the appearance of the putative descendant in (b), the trend in the ancestor is reversed so that the net change is nil. In (c) and (d), statistically significant trends in the ancestor species are irrelevant in either time (c) or morphological direction (d) to the earliest representatives of the putative descendants. (Modified from Cheetham 1987.)

of stasis, at least among marine invertebrates, although a number of gradually evolving lineages have been documented by multivariate studies as well (see Jackson and Cheetham 1999). The role of directional selection in gradual patterns appears obvious, although, in practice, the rate of change may not be rapid enough to require anything more than the accumulation of non-deleterious mutations at a rate consistent with the average measured in many groups of organisms. The genetic basis for stasis is more complicated, and its evolutionary implications are only beginning to be understood.

Standard quantitative genetic tests based on reconstructed genetic parameters in fossil species of *Metrarabdotos* suggest that random genetic drift, acting on a background of mutation at average rates, is sufficient to account for all of the fluctuation in morphology within species (see Cheetham *et al.* 1995). It is thus unnecessary to explain fluctuation as the result of tracking fine-scale environmental change by (directional) selection. On the other hand, it does become necessary to invoke (stabilizing) selection to account for the virtual lack of net change in intraspecies morphology, in terms of standard quantitative genetic theory. In this situation, stabilizing selection can be viewed as an 'adaptive gridlock' resulting from conflicting demands on an organism's functions and the genetic correlation among characters (Vermeij *in* Kerr 1995).

One problem with invoking stabilizing selection for millions of years as an explanation for widespread within-species stasis is that the pool of genetic variation from which a descendant species might be differentiated would thereby be depleted, perhaps more rapidly than it could be replenished by mutation. However, there is a mechanism for conserving genetic variation under selection: phenotypic plasticity, i.e. the differential abilities of genotypes to produce suites of phenotypes under environmental cues. If the latitudes of phenotypic variability (i.e. degrees of plasticity) of different genotypes are themselves heritable, genotypes become more elusive as targets of selection. The ubiquitous within-colony morphological variability in bryozoans is an obvious possibility for phenotypic variation that might have this effect. Breeding experiments with living species have shown that within-colony variability in many characters includes a significant heritable component and thus qualifies as true phenotypic plasticity (Cheetham *et al.* 1995). Genetic variation in bryozoans appears to be conserved at the same high level as in other sexually reproducing taxa such as *Drosophila*, possibly because of this ability.

If stabilizing selection does predominate through the history of most species, would the morphological differentiation associated with their origins require intermittent, geologically brief episodes of directional selection? For *Metrarabdotos* and other bryozoans showing patterns of morphological evolution consistent with the punctuated equilibria model, overall rates of change appear to require only the accumulation of mutations and random genetic drift, with no necessary input from directional selection (Cheetham and Jackson 1995). It is true that stratigraphic resolution no better than hundreds of thousands of years may be insufficient to estimate the real speed with which species differentiate, and that directional selection may indeed be a requirement. However, according to quantitative genetic theory, mutation and drift would be most effective as diversifying forces in populations with near-optimum phenotype as the result of stabilizing selection. Near the optimum, differences in fitness are comparatively small, allowing rapid drift, but farther from the optimum, the sharper decline in fitness forces the population back, unless an isolating mechanism intervenes to separate gene pools (i.e. speciation). Alternatively, Mayr's model of speciational evolution in small, peripherally isolated founder populations does involve directional selection as its second step, after the

generation of novel gene combinations (the 'genetic revolution'; Mayr 1992).

Conclusion

Given the centrality of stasis in the continuing debate over evolutionary tempo and mode, one may wonder why, decades after the exhortation to regard stasis as data (Gould and Eldredge 1977), so much remains to be done to establish its relative incidence. The answer, of course, lies in the strict requirements for identifying stasis. As a property of virtually the whole of a species' duration, measurable on average in millions of years, stasis necessarily is identified from palaeontological data, and thus is based on morphospecies. The first requirement is for assurance that the correspondence between morphospecies and biological species is high. By testing the genetic differences between extant representatives of species discriminated on the basis of characters observable in fossils, procedures can be established for the use of morphology to discriminate extinct species. Experience suggests that the biological significance of morphospecies is in general improved by taxonomic splitting to the maximum extent allowed by statistical significance.

Evolutionary stasis is a relative condition, and thus not identifiable simply by tracking morphological change in one or more morphological characters through the stratigraphic range of a species. Therefore, the second requirement is for a hypothesis of phylogenetic relationship between species to provide a suitable standard of interspecific difference with which to compare the tempo of change within species. Moreover, it is not just the rates of change and their morphological directions that are important. Stasis is implicitly linked to hypotheses of evolution at the species level, and thus the measurement of changes within and between species should emphasize those aspects of overall morphology that distinguish the species from each other.

A third requirement is for adequate sampling, not just stratigraphically and geographically, but morphologically as well. In addition to their importance in resolving the tempo of change within species, stratigraphic data are needed for choosing among alternative hypotheses of phylogenetic relationship. Such relationships are required not only to determine the timing and morphological polarity of interspecific differences, but also to establish whether ancestor and descendant species overlap on a geological time scale (persistence criterion). Likewise, single morphological characters provide only samples of the overall morphological changes within and between species, and are thus subject to the same principles of statistical inference as the number and spacing of stratigraphic levels at which a species occurs.

Only by continuing to accumulate evidence based on palaeontological data meeting these requirements can the relative incidence of stasis be resolved. Data from a number of taxonomic groups suggest that the fossil record is up to the challenge (Donovan and Paul 1998). The results are important not only for understanding evolution at the species level, but also for explaining how patterns of morphological variety (disparity) and taxonomic diversity are generated at all levels (macroevolution).

References

Cheetham, A.H. (1986) Tempo of evolution in a Neogene bryozoan: rates of morphologic change within and across species boundaries. *Paleobiology* **12**, 190–202.

Cheetham, A.H. (1987) Tempo of evolution in a Neogene bryozoan: are trends in single morphologic characters misleading? *Paleobiology* **13**, 286–296.

Cheetham, A.H. and Jackson, J.B.C. (1995) Process from pattern: tests for selection versus random change in punctuated bryozoan speciation. In: D.H. Erwin and R.L. Anstey, eds. *New approaches to speciation in the fossil record*, pp. 184–207. Columbia University Press, New York.

Cheetham, A.H., Jackson, J.B.C. and Hayek, L.C. (1995) Quantitative genetics of bryozoan phenotypic evolution. III. Phenotypic plasticity and the maintenance of genetic variation. *Evolution* **49**, 290–296.

Cheetham, A.H., Jackson, J.B.C., Sanner, J. and Ventocilla, Y. (1999) Neogene cheilostome Bryozoa of tropical America: comparison and contrast between the Central American Isthmus (Panama, Costa Rica) and the north-central Caribbean (Dominican Republic). *Bulletins of American Paleontology* **357**, 159–191.

Donovan, S.K. and Paul, C.R.C., eds. (1998) *The adequacy of the fossil record*. John Wiley and Sons, Chichester.

Gould, S.J. and Eldredge, N. (1977) Punctuated equilibria: the tempo and mode of evolution reconsidered. *Paleobiology* **3**, 115–151.

Jackson, J.B.C. and Cheetham, A.H. (1994) Phylogeny reconstruction and the tempo of speciation in cheilostome Bryozoa. *Paleobiology* **20**, 407–423.

Jackson, J.B.C. and Cheetham, A.H. (1999) Tempo and mode of speciation in the sea. *Trends in Ecology and Evolution* **14**, 72–77.

Kerr, R.A. (1995) Did Darwin get it all right? *Science* **267**, 1421–1422.

Levinton, J. (1988) *Genetics, paleontology, and macroevolution*. Cambridge University Press, Cambridge.

Mayr, E. (1992) Speciational evolution or punctuated equilibria. In: A. Somit and S.A. Peterson, eds. *The dynamics of evolution*, pp. 21–53. Cornell University Press, Ithaca.

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2.1.3 Rapid Speciation in Species Flocks

A.R. McCUNE

Introduction

Evolution on island archipelagos of closely related endemic species, such as the Galapagos finches or Hawaiian fruit flies, has been an important focus for evolutionary biologists from the time of Darwin and Wallace to the present day. Like oceanic islands, however, certain inland lakes—islands in a sea of land—host impressive endemic radiations of fishes and invertebrates, including gastropods, ostracods, and amphipods (Martens 1997). These species flocks, or complexes of closely related species endemic to geographically limited areas, pose important questions about the tempo, mode, geography, and ecological context of speciation, extinction, and evolutionary change. Lacustrine faunas, in particular, provide an exceptional opportunity for studying the tempo of evolution because lakes produce highly continuous sedimentation that can sometimes provide temporal resolution at scales as fine as individual years.

Some of the most spectacular examples of species flocks are fishes, such as the cichlid fishes in lakes Malawi and Victoria, where hundreds of species endemic to each lake exhibit myriad colours, forms, behaviours, and trophic adaptations. Less familiar are endemic radiations of non-cichlid fishes such as killifishes from Andean Lake Titicaca, pupfishes from Lake Chichancanab, Mexico, minnows from Lake Lanao of the Philippines, sculpins from Lake Baikal, and semionotid fishes from Mesozoic lakes in eastern North America (Echelle and Kornfield 1984). Study of living species flocks has produced greater understanding of the role of ecology and behaviour in the evolution of these fishes, although recent extinctions, among Victoria cichlids and Lanao cyprinids, for example, are vastly reducing our ability to gain further ecological insights (Echelle and Kornfield 1984; Martens 1997). Fossil semionotid fishes exhibit analogous morphological diversity (Fig. 2.1.3.1), and their study complements neontological research by documenting the acquisition of evolutionary novelties through time by species and clades, and then localizing the appearance of novelties to periods of lake expansion (see McCune 1997). All these examples considered together suggest a rather general phenomenon of intralacustrine speciation by fishes under circumstances not readily explained by allopatric speciation.

Speciation in cichlids is commonly touted as rapid or even 'explosive.' Indeed, recent palaeolimnological evidence suggests that in Lake Victoria a clade of more than 300 cichlid species arose as little as 12400 years ago (see Martens 1997). Despite wide latitude in interpretations of the meaning of 'rapid', surely all would agree that African cichlids have speciated rapidly. When comparable measures of the rate of speciation are used, it becomes clear that rapid speciation is not only common among cichlids, but also characteristic of other species flocks of fishes, irrespective of whether the fishes are extant or extinct and whether the time of origin of a clade is estimated from geological data or rates of DNA sequence divergence. Furthermore, speciation in lacustrine species flocks of fishes appears to be more rapid than in other radiations of animals, including fruit flies on Hawaii (McCune 1997; McCune and Lovejoy 1998).

Speciation rate and the time for speciation

What constitutes rapid speciation and how should it be measured? Perhaps most commonly, speciation rate (SR) is a measure of diversification, i.e. the number of species, per ancestral species, that arise within a clade per unit time:

$$SR_{log} = (\ln n)/t \quad (1)$$

where SR_{log} is a logarithmic estimate of speciation rate, n is the number of species in a clade, and t is the age of that clade. A related but distinct quantity of interest is how much time is required for speciation, i.e. how long does it take for reproductive isolation to evolve? Time required for speciation, viewed as the evolution of reproductive isolation, is a process that can involve varying degrees of prezygotic isolation (i.e. events occurring before fertilization that lead to reproductive isolation), as well as hybrid inviability or sterility (postzygotic isolation). The time it takes for populations to develop reproductive isolation has been examined by Coyne and Orr (1989), who analysed data on genetic distance, prezygotic isolation, and postzygotic isolation and estimated that 1.5–3.5 myr is required for speciation in *Drosophila*.

In addition to the study of reproductive isolation, time for speciation (TFS) can be estimated taxically using the logarithmic model:

$$TFS_{log} = (t \ln 2)/\ln n \quad (2)$$

where t is the age of a clade and n is the number of species within the clade (McCune 1997). Logarithmic estimates of SR and TFS, as defined above, assume a phylogenetic topology which is symmetrical or balanced, and fully branched dichotomously (Fig. 2.1.3.2a). But if a particular phylogeny is more comb-shaped (i.e. speciation rates vary within a clade or that some lineages are better speciators) as depicted in Fig. 2.1.3.2(b), linear models of SR and TFS, given by the equations

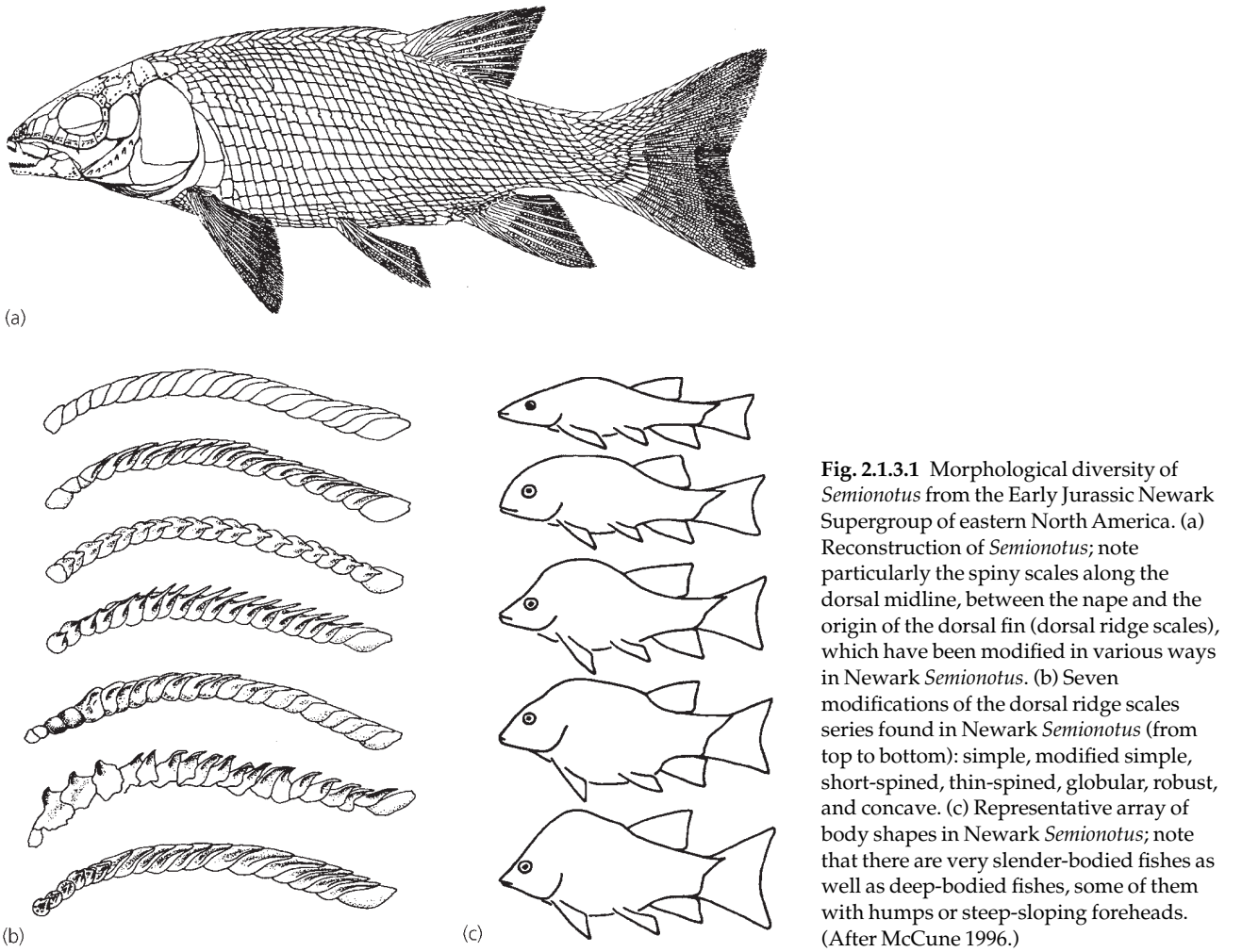

Fig. 2.1.3.1 Morphological diversity of *Semionotus* from the Early Jurassic Newark Supergroup of eastern North America. (a) Reconstruction of *Semionotus*; note particularly the spiny scales along the dorsal midline, between the nape and the origin of the dorsal fin (dorsal ridge scales), which have been modified in various ways in Newark *Semionotus*. (b) Seven modifications of the dorsal ridge scales series found in Newark *Semionotus* (from top to bottom): simple, modified simple, short-spined, thin-spined, globular, robust, and concave. (c) Representative array of body shapes in Newark *Semionotus*; note that there are very slender-bodied fishes as well as deep-bodied fishes, some of them with humps or steep-sloping foreheads. (After McCune 1996.)

$$SR_{lin} = n/t \quad (3)$$

$$TFS_{lin} = t/(n-1) \quad (4)$$

will yield more accurate estimates. The resulting values will be faster and shorter than corresponding logarithmic estimates of SR and TFS. In reality, phylogenetic topology for most clades is probably somewhere between (e.g. Fig. 2.1.3.2c; Heard 1996). Here, however, the more conservative, logarithmic estimates of SR and TFS are used. Note also that all taxic estimates of SR and TFS reflect net speciation and will thus tend to underestimate gross SR and overestimate TFS.

Geological and molecular dating of clade origin

Estimates of both SR and TFS depend critically on estimates of clade age t. For most species flocks of fishes, estimates of clade age have been based on the age of the lake basin inhabited by that particular clade. The age of basin origin provides a maximum estimate of clade age because basin formation may substantially precede lake formation, and there may be a further significant delay before a newly formed lake is colonized by fishes. The disparity between basin age and lake age is well illustrated by the case of Lake Victoria. The maximum age of Lake Victoria cichlids has long been reported as about 200 000 years, based on geological estimates for the age of the Victoria basin, but recent sedimentological and seismic studies have demonstrated that the basin was completely dry only 12 400 years ago (see Martens 1997). Thus, if the Victoria cichlid clade originated in the current Lake Victoria, it can only have existed for 12 400 years. The most refined estimates of lake age are derived from sedimentological studies, either direct examination of cores or seismic profiles, rather than biostratigraphic studies or radiometric dating of volcanics. Unfortunately, sedimentological data from cores have not been obtainable for many lakes given the great depth of some lakes, the substantial thickness of lacustrine sediments,

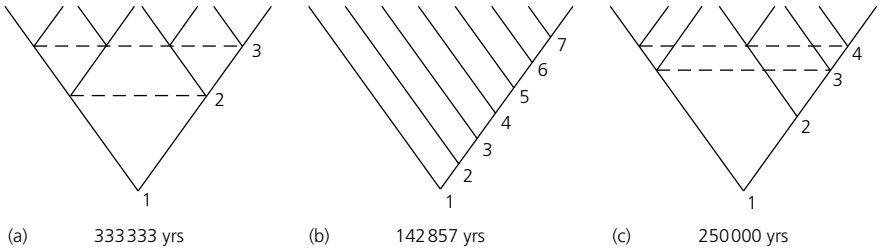

Fig. 2.1.3.2 Variation in TFS with phylogenetic topology. For a hypothetical case of eight species arising in 1 myr, TFS varies from 143 000 to 333 333 years, depending on topology (if there is no phylogenetic resolution, as for a polytomy, TFS = 1 myr). Simultaneous episodes of divergence are indicated by a dotted line and numbered, and the estimated TFS is given below each cladogram. (a) For a balanced, fully resolved phylogeny, there are three episodes of divergence, yielding an estimated TFS of 333 333 years per speciation event (equivalent to the TFS_{log} estimate for eight species). (b) A comb-like phylogeny gives the shortest estimated TFS of approximately 143 000 years (equivalent to the TFS_{lin} estimate for eight species). (c) An example of one of many intermediate phylogenies, where four episodes of divergence yield a TFS of 250 000 years.

and the logistic difficulties of drilling in remote inland and/or mountainous areas.

Since the 1990s the ease of generating DNA sequence data from living organisms has provided an exciting alternative to geological data for dating clade origins. Using DNA sequence data to derive estimates of clade age, however, involves a number of assumptions, including calibration of relative rates through application of the controversial 'molecular clock' (see Section 5.3.6). It is clear that different genes in the same taxa and the same genes in different taxa evolve at different rates, and that parameters like body size, generation time, and metabolic rate may influence rates of divergence (see review by Avise 1994). Furthermore, any absolute calibration of rates of DNA sequence divergence depends, at some level, on geologically derived dates. Despite these problems, in some cases, where both refined sedimentological techniques and DNA sequence data have been obtained to estimate lake age and clade age respectively, there can be remarkable agreement. For example, a clade of up to five species of pupfish in Lake Chichancanab in the Yucatan of Mexico has been dated as about 8000 years old, based on studies of DNA sequence divergence. Sedimentological studies show that 8000 years ago, the basin was completely dry (see McCune 1997).

The molecular methods of dating clade age discussed above are pertinent only to living species flocks of fishes. There are, however, exceptional fossil species flocks—semionotid fishes from Early Jurassic lakes in the Newark Supergroup of eastern North America—which are dated remarkably precisely owing to the nature of the sedimentary record. The Newark lacustrine record consists of Milankovitch cycles which reflect, within each of several basins, a succession of episodes of lake formation and evaporation, controlled by climatic change. Within individual cycles of lake formation and evaporation, sediments are deposited as annual couplets called varves. Thus, it has been possible, through studies of species distributions in time and space, to determine probable sites and times of origin, and to calculate a relatively precise maximum estimate of TFS for a number of endemic species (McCune 1996). Stratigraphic resolution between successive lake cycles is about 22 000 years, and within the varved sequences of individual lake episodes, microstratigraphic position has been determined to within decades. TFS for these fossil semionotid fishes is comparable to that for the most rapidly speciating living fishes (McCune 1997).

How fast have species flocks of fishes speciated?

As palaeolimnological dating of lakes and analyses of DNA sequence data have become more refined, estimated ages of lakes and clades have tended to decrease, thus yielding faster estimates of the rate of speciation in species flocks of fishes. Logarithmic estimates of TFS suggest that, on average, speciation in species flocks of fishes has taken only 0.002–0.3 myr (see Table 2.1.3.1), with the exception of Tanganyikan cichlids, which may have diverged much more slowly. In general, the estimated TFS_{log} for species flocks of fishes is at least two to four times faster than for other fishes (McCune and Lovejoy 1998). Comparison of TFS_{log} for species flocks of fishes with island radiations of arthropods and birds also seems to reveal more rapid speciation by these fishes (Table 2.1.3.1). There are a variety of biases that could produce the higher TFS_{log} (and lower SR_{log}) for the island radiations, however, so the apparent difference in TFS_{log} must be viewed with caution. The dating of lake origins may be more precise than that of islands, leading to overestimates of TFS_{log} for island radiations (for further discussion, see McCune 1997). Thus, the lower SR_{log} and longer TFS_{log} for island radiations could be an artefact of

Table 2.1.3.1 Speciation rates (SR_{log}) and time for speciation (TFS_{log}) for endemic fishes within lakes and animals on islands. Sources for island arthropod and bird data are given by McCune 1997. For fishes, estimates span both the maximum and minimum estimated ages of lakes (see McCune 1997). SR and TFS are expressed as logarithmic estimates (see text for definition). Sedimentological dates for lake origin were favoured over stratigraphic dates for basin origins. Where the number of endemics is marked by an asterisk, monophyly has not been demonstrated, so these complexes are treated as individual lineages (i.e. five species originating in 4000 years is treated as each of five species having originated in 4000 years).

Lake or island	Taxon	Endemics (no. species)	Age (myr)	SR_{log} (myr)	TFS_{log} (myr/sp.)
Lake Victoria	Cichlids	300	0.012–0.2	28–475	0.002–0.024
Lake Nabugabo	Cichlids	5*	0.004	—	0.004
Lake Malawi	Cichlids	400	0.7–2.0	3–9	0.081–0.231
Lake Tanganyika	Cichlids—Tropheini	6	1.2–12.0	0.75–1.49	0.464–4.642
Lake Tanganyika	Cichlids—Ectodini	30	2.4–12.0	0.28–1.42	0.489–2.446
Lake Tanganyika	Cichlids—Lamprologini	85	2.4–12.0	0.37–1.85	0.374–1.87
Barombi Mbo	Cichlids	11	1.0–1.1	2.2–2.4	0.289–0.318
Lake Titicaca	Cyprinodontids	~22	0.02–0.15	3.8–155	0.004–0.179
Lake Chichancanab	Cyprinodontids	5	0.008	201	0.0034
P4, Newark Basin	Semionotids	6*	0.005–0.008	—	0.005–0.008
Hawaiian Islands	Crickets	250	5.6	0.99	0.703
Hawaiian Islands	Drosophilids	860	5.6	1.21	0.574
Hawaiian Islands	Honeycreepers	47	5.6	0.69	1.008
Hawaiian Islands	Spiders, Tetragnatha	100?	5.6	0.82	0.843
Hawaiian Islands	Plant bugs, Sarona	40	5.6	0.66	1.052
Galapagos Islands	Finches	14	5–9	0.29–0.52	1.3–2.4

the higher t for islands relative to lakes, given the well-known inverse relationship between rates and the interval over which they are measured. Despite possible problems with the island data, however, estimates of TFS_{log} for island radiations (0.6–2.4 myr) are remarkably similar to the 1.5–3.5 myr estimated as necessary for the evolution of reproductive isolation in *Drosophila* (Coyne and Orr 1989). Thus, all the evidence taken together suggests that lacustrine species flocks of fishes have indeed speciated very rapidly.

References

Avise, J.C. (1994) *Molecular markers, natural history and evolution*. Chapman and Hall, New York.

Coyne, J.A. and Orr, H.A. (1989) Pattern of speciation in *Drosophila*. *Evolution* **43**, 362–381.

Echelle, A.A. and Kornfield, I. (1984) *Evolution of fish species flocks*. University of Maine, Orono.

Heard, S. (1996) Patterns in phylogenetic tree balance with variable and evolving speciation rates. *Evolution* **50**, 2141–2148.

Martens, K. (1997) Speciation in ancient lakes. *Trends in Ecology and Evolution* **12**, 177–182.

McCune, A.R. (1996) Biogeographic and stratigraphic evidence for rapid speciation in semionotid fishes. *Paleobiology* **22**, 34–48.

McCune, A.R. (1997) How fast do fishes speciate: molecular, geological, and phylogenetic evidence from adaptive radiations of fishes. In: T.J. Givnish and K.J. Sytsma, eds. *Molecular evolution and adaptive radiation*, pp. 585–610. Cambridge University Press, Cambridge.

McCune, A.R. and Lovejoy, N.R. (1998) The relative rate of sympatric and allopatric speciation in fishes: tests using DNA sequence divergence between sister species and among clades. In: D. Howard and S. Berlocher, eds. *Endless forms: species and speciation*, pp. 172–185. Oxford University Press, London.

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2.2 Evolution of Form

2.2.1 Developmental Genes and the Evolution of Morphology

G.A. WRAY

Introduction

The past two decades have witnessed tremendous advances in our understanding of the genetic basis of form. Numerous genes responsible for patterning morphology, from global features of body organization to fine anatomical details, have been identified in a variety of 'model' organisms, such as fruit flies and corn. Characterizations of these genes have revealed that most encode proteins that control key cellular and developmental processes (Gerhart and Kirschner 1997). Many regulatory genes encode transcription factors, which are proteins that precisely modulate the timing, location, and level of expression of specific genes. Other regulatory genes encode components of intercellular signalling systems: the signals themselves, the receptors for those signals, and the transducing proteins that relay the status of the receptor from the surface to the interior of the cell. All the fundamental processes of development—pattern formation, cell fate specification, morphogenesis, cell division, and differentiation—are controlled by these genes and the proteins that they encode.

The wealth of data emerging about the genetic underpinnings of morphology in 'model' organisms provide information and analytic tools that are invaluable for understanding the evolution of form (Raff 1996). Comparisons of regulatory genes and their functions among distantly related taxa have revealed similarities where none was suspected and have led to the recognition that morphologically disparate taxa often share crucial regulatory genes and developmental processes. Data on developmental regulatory genes have been used to test hypotheses of homology among structures in distantly related taxa, and even to reconstruct the morphology of long-extinct ancestors. Regulatory genes have also been used to explore the genetic basis for evolutionary changes in morphology and for the origin of novel structures.

Shared genetic underpinnings

Much of the information that has emerged from comparisons of regulatory genes among 'model' taxa has come as a surprise. One of the first surprises to emerge was how phylogenetically widespread many regulatory genes actually are (Gerhart and Kirschner 1997). To take a famous example: homeobox genes, which encode transcription factors, were first recognized as playing important developmental roles in fruit flies. The discovery of homeobox genes in vertebrates created a sensation, as it had been widely assumed that the very different body plans of arthropods and chordates would have correspondingly few underlying genetic similarities. It is now clear that many developmental regulatory genes are phylogenetically widespread (Fig. 2.2.1.1). Genes encoding transcription factors are particularly widespread: homeobox, MADS-box, and zinc-finger families are present in plants, animals, fungi, and protists.

Other developmental regulatory genes have a somewhat narrower phylogenetic distribution. For instance, several different proteins that act as intercellular signals during induction are apparently restricted to metazoans. The signalling protein *delta* and its receptor *notch*, for instance, are present in nematodes, arthropods, echinoderms, and chordates, but homologues have not been found outside metazoans. This phylogenetic restriction of several intercellular signalling systems to animals is perhaps not surprising: cell–cell communication is of limited use to unicellular protists, but an important process that is used repeatedly during the patterning of all animal embryos.

A second surprise to emerge from the initial comparisons of regulatory genes among 'model' species was the discovery that many of them regulate similar developmental processes in phylogenetically distant and morphologically disparate species. Again, homeobox genes provided the first dramatic examples. A subset of these genes belonging to the *Hox* complex was found to specify position along the anteroposterior axis in both fruit fly and mouse embryos. Many other developmental regulatory genes are now known to carry out developmental roles that are broadly similar in arthropods and chordates. In a wide range of animal phyla, for instance, transcription factors encoded by *myoD* determine the differentiation of muscle cells and those encoded by *achaete–scute* the fate of sensory neurones. These and other examples suggest that, at least in some cases, a particular regulatory gene can continue to control the same developmental process for hundreds of millions of years.

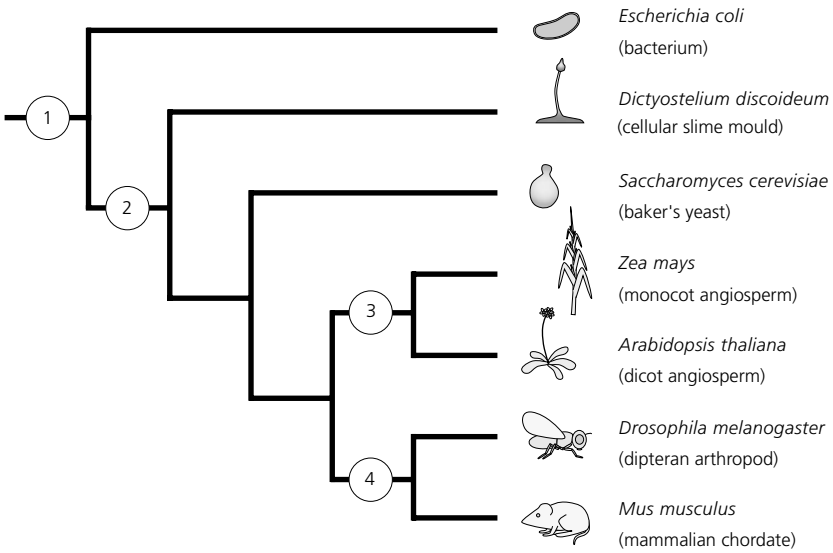

Fig. 2.2.1.1 Antiquity of regulatory genes. Many developmental regulatory genes are shared among distantly related organisms. All living species share numerous metabolic processes and basic features of cell biology (1), but prokaryotes and eukaryotes share relatively few regulatory genes. Throughout unicellular and multicellular eukaryotes, however, homologous regulatory genes are surprisingly widespread (2). Those encoding several families of transcription factors are widely present, including homeobox and MADS-box genes. This suggests that precise and complex gene regulatory systems were present long before multicellular life evolved. Metaphytes (3) have put some of these regulatory genes to unique uses. For instance, MADS-box transcription factors are used to pattern inflorescences in angiosperms. Metazoans (4) have also adopted transcription factors to unique uses, most famously the homeobox genes for patterning the anteroposterior axis. Metazoans have also evolved what are apparently entirely new regulatory systems, in the form of intercellular signalling systems. (For discussion and references, see Gerhart and Kirschner 1997.)

New roles for old genes

An exclusive association between a particular regulatory gene and a specific developmental process is not the rule, however. A third surprise was the discovery that regulatory genes can control several different developmental processes within single species. In *Drosophila*, for instance, the *delta/notch* signalling system is essential for the development of eyes, sensillae, and wings, while the transcription factor *engrailed* is needed during the development of segment boundaries, the gut, and the central nervous system.

A multiplicity of developmental roles for a single regulatory gene seems to be the rule rather than the exception. In retrospect, this is not surprising: there are fewer signalling systems than there are inductive interactions during the development of most animals, and fewer transcription factors than there are genes whose transcription needs to be regulated. It is exceedingly improbable that several different development roles could evolve simultaneously for a single gene. The most reasonable interpretation is that regulatory genes can repeatedly acquire new regulatory roles during the course of evolution, a process known as recruitment.

This conclusion is bolstered by comparisons among species, where the repertoire of developmental roles controlled by a particular gene often differs markedly. To continue with the *delta/notch* example, this signalling system is required for the development of the immune system, feather tracts, and limbs in vertebrates. The sets of developmental processes mediated by this signalling system is almost non-overlapping between arthropods and chordates, an observation that is fairly typical when comparing distantly related taxa. Even when striking similarities do exist in the roles of regulatory genes, as in the nested domains of *Hox* gene expression found in both arthropods and chordates, there are several other developmental roles controlled by the same gene that differ between the two phyla. It seems likely that these regulatory genes recruited new developmental roles following the divergence of arthropods and chordates.

The evolutionary origin of a new developmental role does not always coincide with the origin of a structure. In some cases, it may follow the evolutionary origin of a structure by hundreds of millions of years. A well-studied case concerns the gene *sex-lethal* (Fig. 2.2.1.2a). This gene is the master regulatory gene of sex determination throughout the genus *Drosophila* but has no role in this process in many other genera of flies. Separation of the sexes, with attendant sexual dimorphism, is clearly older than the evolution of flies within the insects, sug-

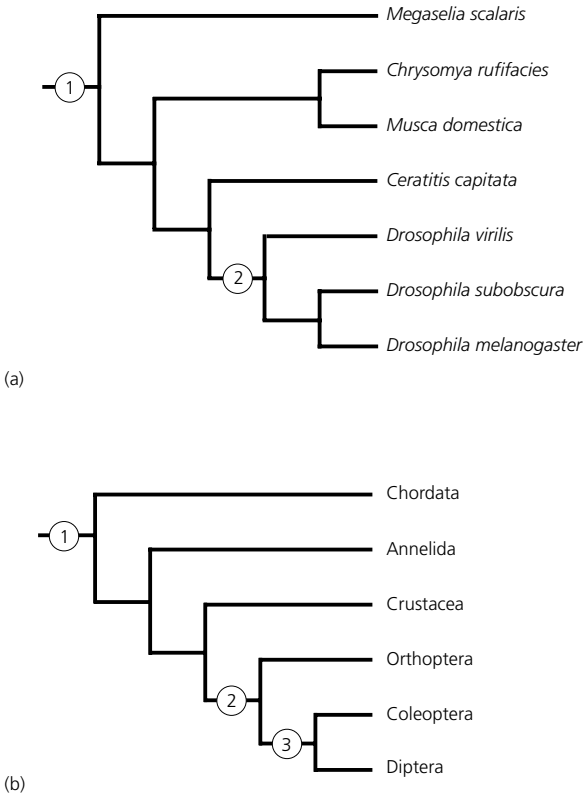

Fig. 2.2.1.2 Decoupled evolution of regulatory genes, developmental roles, and morphology. (a) The gene *sex-lethal* is present throughout the Diptera (flies), and probably predates the origin of this clade (1); in the genus *Drosophila*, *sex-lethal* is the key regulatory gene in the sex determination process (2). Since separate sexes evolved much earlier (1), the eponymous role of *sex-lethal* in sex determination is almost certainly a relatively recent evolutionary acquisition. All the taxa listed are flies of various sorts. (b) Like all the other *Hox* cluster genes, *Hox-3* is a homeotic gene that is involved in specifying position along the anteroposterior axis in most animals (1); in some insects, however, *Hox-3* has lost this role (3); in all insects, *Hox-3* is expressed in the extra-embryonic membranes during early development, a role unique to arthropods. (For discussion and references, see Wray 1998.)

gesting that *sex-lethal* acquired its regulatory role in sex determination long after sex determination evolved.

The opposite situation, where a regulatory gene loses a developmental role but the structure remains, can also occur. A case in point is the *Hox-3* (*zen*) gene of insects (Fig. 2.2.1.2b). In most phyla, this member of the *Hox* complex is involved in patterning position along the anteroposterior axis. This is the case in basal insects, such as grasshoppers, but not in more derived groups, such as beetles and flies. Since these derived groups retain an anteroposterior axis with anatomically distinct segments, it is clear that the ancestral patterning role of this gene has been lost. In all insects that have been examined, *Hox-3* has a role in the development of the extra-embryonic membranes, so the gene has been retained despite the loss of its plesiomorphic role within insects.

Versatile genes, diverse morphology

Not only do most regulatory genes control several developmental processes, but these processes can be functionally quite distinct from one another. This regulatory versatility is apparent within the ontogenies of single species as well as in comparisons across taxa. During the development of *Drosophila melanogaster*, for instance, *engrailed* regulates segmental patterning and neuronal cell fate specification, which are two very different kinds of developmental processes. Similarly, *Leafy* regulates the patterning of leaf primordia in angiosperms while a member of the same gene family, *SRY*, regulates sex determination in mammals.

These and many other examples highlight the fact that regulatory genes are functionally neutral switches: it is not a regulatory gene itself, but rather the genes whose activity it controls, that actually produces form. A given transcription factor may trigger cell division in one species and cell death in another, while a cell signalling system may induce the differentiation of neurones in one species and gastrulation in another. Indeed, the very antiquity of many regulatory gene families strongly suggests that most, and perhaps all, of their developmental roles in living taxa are not their original ones. For instance, it is only in animals that homeobox genes specify position along the anteroposterior axis, and only in plants that MADS-box genes perform an analogous function. Yet both gene families are present in both clades (Fig. 2.2.1.1) and were surely present in their single-celled ancestors, which had no need of patterning groups of cells. It is likely that each gene family acquired their famous patterning roles independently, one following the origin of land plants and the other following the origin of animals.

Genes as indices of morphological homology

The discovery that many regulatory genes are associated with conserved developmental processes in distantly related taxa suggests an important application of genetic data to evolutionary studies. This is the use of regulatory gene expression as an index of homology for morphological structures. The basic idea is simple: since regulatory genes control the production of morphology, and since their association with particular aspects of the phenotype can be quite evolutionarily conservative, they should be reliable guides to morphological homology.

This approach has been applied successfully to a number of classical problems in the evolution of morphology. One is the origin of the vertebrate brain. Several

regulatory genes, including *Hox* genes and *orthodenticle*, are known to be expressed in homologous regions of the brain in diverse vertebrates. By examining where these genes are expressed in the brains of an ascidian and a cephalochordate (amphioxus), it has been possible to work out regional homologies between the relatively simple brains of these invertebrate chordates and vertebrates (Williams and Holland 1998). This analysis has shed light on the evolutionary transformation in morphology. Other interesting applications of regulatory gene expression data to testing hypotheses of morphological homology include the identification of serially homologous tagma and segments in various groups of arthropods using *Hox* genes (Averof *et al.* 1996).

However, not all similarities in gene expression reflect conserved developmental roles that were present in a common ancestor (Wray 1998). Another possibility, though seldom discussed, is that gene expression can be convergently similar. Some likely cases are now known. For instance, various components of the *delta/notch* signalling system are expressed in strikingly similar patterns in tetrapod limbs and insect wings (Shubin *et al.* 1997). It is clear from the fossil record and from comparative anatomy that these structures are not homologous. The most plausible interpretation is that the similarity in gene expression is due to the independent application of a conserved developmental 'subroutine'. Another likely case concerns the gene *distal-less*, which is expressed in the distal portion of developing appendages of arthropods, vertebrates, annelids, echinoderms, and ascidians. Again, these appendages are not homologous, and it seems likely that the gene is part of a conserved developmental subroutine that has been utilized during the evolutionary origin of many different appendages (Fig. 2.2.1.3).

Genes like *notch*, *delta*, and *distal-less* are clearly poor choices for testing hypotheses of homology among appendages for this reason. Other regulatory genes may prove misleading because they control the differentiation of cell types. For instance, *myoD* regulates muscle cell differentiation throughout the body, and would not be useful to test whether a certain region of the body in one species is homologous to a body region in another species. In addition to these problems, there is the further complication that most regulatory genes control several different developmental processes. This means there is the possibility of comparing developmental roles that evolved on separate occasions (i.e. convergently) rather than those that are conserved, which could also be misleading.

Although regulatory genes offer great promise as indices of homology, they are not infallible. If used with appropriate caution, they are likely to prove useful in unravelling homologies of anatomical features that would otherwise be very difficult to recognize with confidence. In general, the more closely related two species are, the more developmental roles they will share for any given regulatory gene and the more reliable will be inferences about morphological homology based on these genes.

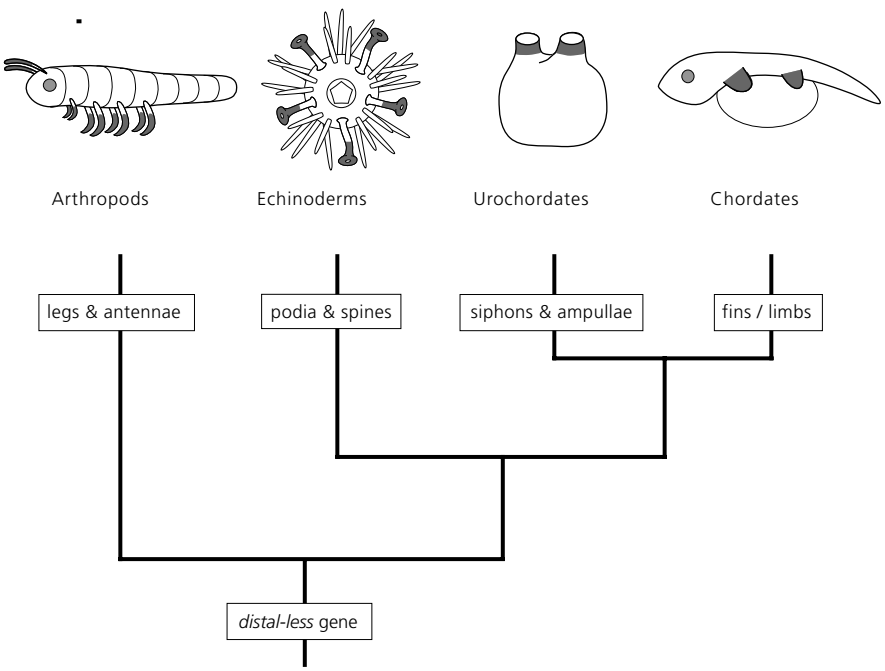

Fig. 2.2.1.3 Parallel application of a conserved developmental role. The gene *distal-less* is present throughout the Bilateria. In several different phyla, this gene is expressed in the distal portion of developing outgrowths of various kinds. These structures are not, however, themselves homologous. It seems unlikely that the same gene would be expressed in a similar fashion in non-homologous organs by chance. Instead, it is likely that *distal-less* is part of a genetic pathway that patterns secondary axes, and has been independently applied to the development of various kinds of outgrowths on many separate occasions. (For discussion and references, see Shubin *et al.* 1997 and Wray 1998.)

Reconstructing ancestors

The process of using regulatory genes to test hypotheses of homology can be taken a step further. Applied to multiple features in parallel, this approach can be used to reconstruct the general anatomical features of an ancestor. This process is fraught with all of the uncertainties just outlined, but can, when applied judiciously, reveal points of interest.

Reconstructing the ancestor of the bilaterian metazoans has been attempted, based on similarities in gene expression patterns between *Drosophila* and various vertebrates (DeRobertis and Sasai 1996; Gerhart and Kirschner 1997). The first such similarity to be discovered, the role of genes in the *Hox* complex in specifying position along the anteroposterior axis, has already been mentioned. It has been interpreted to mean that the ancestral bilaterian had a body with distinct regions along the anteroposterior axis. Many other similarities in gene expression between arthropods and chordates have since been discovered—so many, in fact, that the list of implied anatomical features in their latest common ancestor has grown alarmingly long (Table 2.2.1.1). If any similarity in gene expression is read literally to imply the presence of that feature in the original bilaterian, this creature would have had not only muscles, a head, and a central nervous system (which would not surprise any comparative anatomist), but also segments, a heart, image-forming eyes, and appendages (which might seem less plausible on the basis of comparative anatomy). It remains to be seen how reliable a guide gene expression is to anatomical homology across such a deep phylogenetic divide. There is reason to believe that some features of gene expression are indeed homologous in insects and vertebrates, while others may well be superficial similarities (Wray 1998).

A second, well-studied example concerns the origin and diversification of vertebrates. The availability of extant organisms that bracket this important transformation, together with a broader phylogenetic sampling, have produced a more detailed and generally more plausible application of gene expression data to identifying anatomical homologies among the relevant taxa (Williams and Holland 1998). Attention has focused on urochordates and amphioxus as representatives of the prevertebrate condition, and on agnathans as exemplars of early vertebrates. As mentioned earlier, the origin of various regions of the brain has been particularly well studied. Attention has now shifted to understanding the origin of other characteristic vertebrate features, including the notochord, somites, neural crest, and skeleton.

Genes and the evolution of form

It has long been recognized that developmental regulatory genes are a likely locus of mutations that alter morphology in substantive, yet functionally integrated, ways (reviewed by Raff 1996). At least in principle, expanding or contracting the region where a regulatory gene is expressed in an embryo could have the effect of changing the size of a structure. Similarly, changing the location of expression could alter the position of that structure, while establishing a new locus of expression might result in its duplication. These kinds of changes are particularly interesting because the resulting anatomical changes might be functionally integrated. All the developmental processes controlled by the regulatory gene would be activated or repressed in the new spatial pattern, and if the gene were sufficiently far up the regulatory hierarchy, this could mean that several, functionally interacting cell types or structures could be correctly positioned relative to each other.

There are many cases known where the expression profile of a regulatory gene has changed evolutionarily, such that it is active at a different time or in a different cell type or spatial pattern (Carroll 1995; Lowe and Wray 1997). In some cases, these differences correlate with important anatomical features. In arthropods, for example, the regulatory genes that demarcate segments are expressed in the same number of stripes in embryos as there are segment boundaries in the larvae and adults. These kinds of changes in the expression domains of regulatory genes should not be particularly difficult to achieve. Mutations in the promoter region near a gene,

Table 2.2.1.1 Inferring features of the protostome/deuterostome ancestor from genes. (For discussion and references, see Raff 1986 and Gerhart and Kirschner 1997.)

Gene(s)	Shared developmental roles	Inferred feature
Hox complex	Specifies position along AP axis	Regionalized AP axis
sog, chordin	Establish DV axis	DV axis
otx, emx	Specify head region of body	Cephalization
forkhead	Specifies cells around mouth, anus	Through-gut
tinman	Specifies heart cells	Circulatory system
netrin	Specifies midline CNS neurones	Midline nerve cord
achaete–scute	Specifies neurones	Neurones
myoD, myogenin	Specify muscle cells	Muscle cells

AP, anteroposterior; CNS, central nervous system; DV, dorsoventral.

which contains binding sites for transcription factors that control its expression, can alter that expression.

Recruitment is a second kind of evolutionary change involving regulatory interactions that may be important for understanding the evolution of form. This phenomenon involves changes in the developmental processes that are controlled by a given regulatory gene (Averof *et al*. 1996; Lowe and Wray 1997). It may come to interact with more or fewer 'target' genes whose activity has a direct structural or physiological effect.

Many probable examples have been documented. For instance, *brachyury* is involved in the development of the notochord in chordates, a structure that is unique to this clade. The gene, however, is clearly much older than chordates, as it is present in arthropods and echinoderms. In these other phyla, *brachyury* is expressed in a variety of structures, none of which can plausibly be interpreted as a precursor, or homologous to, the notochord. The most reasonable interpretation is that *brachyury* acquired its role in notochord development some time after echinoderms and chordates last shared a common ancestor. Other examples include derived roles for *Hox* genes in vertebrate limbs, *distal-less* in echinoderm podia, and *decapentaplegic* in insect wings.

Conclusion

The deluge of information on the development of global body organization and distinct anatomical structures in 'model' organisms is proving an unintended boon to students of the evolution of form. It is still not possible to identify all the genetic changes that were responsible for a particular anatomical change in evolution. Interactions among regulatory genes are immensely complex, and it is unlikely that it will ever be possible to determine exactly which mutations produced a complex morphological change. Only some of the technical tools needed to study gene interactions can be applied to comparative studies, and those that can are expensive and time-consuming. None the less, it is possible to identify some of the genes that may have contributed to a particular morphological change. This approach has been successfully applied to several anatomical transformations of wide interest, such as the origin of insect wings, the vertebrate brain, and tetrapod limbs.

References

Averof, M., Dawes, R. and Ferrier, D. (1996) Diversification of arthropod *Hox* genes as a paradigm for the evolution of gene functions. *Seminars in Cell and Developmental Biology* **7**, 539–551.

Carroll, S.B. (1995) Homeotic genes and the evolution of arthropods and chordates. *Nature* **376**, 479–485.

DeRobertis, E.M. and Sasai, Y. (1996) A common plan for dorsoventral patterning in Bilateria. *Nature* **380**, 37–40.

Gerhart, J. and Kirschner, M. (1997) *Cells, embryos, and evolution*. Blackwell Science Ltd, New York and London.

Lowe, C.J. and Wray, G.A. (1997) Radical alterations in the roles of homeobox genes during echinoderm evolution. *Nature* **389**, 718–721.

Raff, R.A. (1996) *The shape of life*. University of Chicago Press, Chicago.

Shubin, N., Tabin, C. and Carroll, S. (1997) Fossils, genes and the evolution of animal limbs. *Nature* **388**, 639–648.

Williams, N. and Holland, P.W.H. (1998) Molecular evolution of brain of chordates. *Brain, Behavior and Evolution* **52**, 177–185.

Wray, G.A. (1998) Evolutionary dissociations between homologous genes and homologous structures. In: B.K. Hall, ed. *Homology*, pp. 189–202. Wiley, Chichester.

2.2.2 Constraints on the Evolution of Form

P.J. WAGNER

Introduction

Constraints are factors that limit the range of morphologies that can evolve within a taxon. Numerous evolutionary studies have examined mechanisms of constraint as well as the patterns that suggest differences in levels of constraint among taxa. The study of processes constraining morphological evolution is usually limited to neontology. However, constraint hypotheses predict large-scale patterns that palaeobiologists can observe. The patterns sometimes vary among hypotheses, allowing palaeobiologists to reject one or more constraints. These large-scale patterns include limitations on: (1) magnitudes of morphological transitions; (2) possible morphological transitions; and (3) the 'size' of occupied morphospace. A fourth issue concerns temporal changes in these three limitations. Palaeontological studies that examine morphological variation within species, and morphospace occupation and phylogenetic relationships among species, offer the potential to test hypothesized changes in constraints over time or differences in constraints among related taxa. Palaeontological data can sometimes test not only general hypotheses (e.g. whether constraints increased over time) but also more specific constraint hypotheses (e.g. whether a particular constraint type increased over time).

Types of constraint

Constraints on form have been identified as 'phylogenetic', 'developmental', 'ontogenetic', and 'ecological', among others. Imprecise usage and/or overly general definitions of some terms (especially 'phylogenetic' and 'developmental' constraints) have rendered them almost meaningless. However, there is a basic distinction between intrinsic and extrinsic constraints. Intrinsic constraints affect the potential morphological variation within a taxon, irrespective of ecological variables. Developmental interactions among homologies offer an example. Individual homologies rarely develop independently, if only because of simple physical proximity to other homologies and the need to retain biomechanically feasible morphologies. Genetic effects such as pleiotropy (i.e. the same genes affecting two or more homologies) increase these interactions. When characters are genetically/developmentally linked, then change in one homology necessitates either change or accommodation by one or more additional homologies. Unless these secondary changes or accommodations are at least selectively neutral, developmental/genetic links can constrain morphological evolution against even fairly strong selection (Wright 1978).

Extrinsic constraints are those imposed by the environment that limit variation within a taxon to less than the potential variation. The availability of niches (i.e. the 'vacancies' in ecospace) and the stringency of stabilizing selection are primary examples. A mechanically inflated balloon in a box offers an apt analogy. The maximum size of inflation is intrinsically constrained by elastic properties of the balloon and the pumping properties of the inflating mechanism. The dimensions of the box provide extrinsic constraints, which can limit balloon dimensions regardless of the intrinsic properties.

The simple dichotomy between intrinsic and extrinsic constraints is blurred by the observation that basic trophic strategies and other ecological variables are usually similar among closely related species and can even be described as synapomorphies and symplesiomorphies. However, although ecological and environmental factors tend to be similar among closely related species, these factors can change abruptly without revising any intrinsic limitations on possible evolution. The emptying and subsequent rapid refilling of ecospace around mass extinctions predict altered extrinsic constraints and thus consequent changes in morphological evolution without requiring changes in intrinsic constraints. Crinoid evolution over the Permo-Triassic extinction offers an example of both intrinsic constraints and relaxed extrinsic constraints (Foote 1999). Crinoids witnessed a major morphological diversification (possibly from a single ancestral species) following the end-Permian extinctions. However, survivors remained morphologically stereotyped for features that varied widely among early Palaeozoic taxa. A more vexing problem concerns morphologies functionally associated with particular trophic habits, as constraints on such characters might appear to be both intrinsic and extrinsic. In such cases, it may be impossible to determine whether intrinsic constraints limit possible ecospace or extrinsic constraints restrict the range of realized variation to a portion of that possible.

Implications of constraints for macroevolution

Most processes inducing constraints are invisible to palaeobiologists, but the macroevolutionary patterns that result are not. Differing levels of constraint should affect how much morphological change can accrue over a given amount of time or number of speciation events. Within a species, intrinsic constraints that limit the amount of morphological variation limit the amount of change that selection can induce; such constraints also limit the degree to which populations (demes) differ from one another, reducing the effects of drift. The resulting macroevolutionary pattern is limited *step-size* (i.e. the dissimilarity between a daughter species and its ancestor). Changes in such constraints therefore can decrease or increase typical step-sizes without major ecological change. Increased intrinsic constraints might explain the slowing of morphological change after the Cambrian (Valentine 1991 and references therein), whereas decreased intrinsic constraints have been cited as a possible cause of major diversifications (Erwin 1992).

Other constraint hypotheses focus on how many morphologies can evolve (either given a particular ancestral morphology or not). For example, a character might evolve in an ordered series (i.e. character states 2 or 4 can easily evolve into state 3 whereas states 1 or 5 cannot). A very different intrinsic constraint is the limitation of plausible states available to a character (i.e. the number of states is finite). This clearly applies to molecular characters, but was thought not to affect morphological evolution. However, analyses of numerous fossil clades indicate that both ordered evolution and finite states limit the number of discernible states for most clades (Wagner 2000). Differences in the 'tightness' of state ordering and in character state availability obviously can affect the responses of clades to the same ecological conditions, even if the actual step-sizes within two clades are the same.

Extrinsic constraints focus on the relationship between ecological strategy and morphology, and how changes in the availability of new niches affect rates of morphological change. A classic extrinsic constraint hypothesis concerns the Cambrian explosion. Early

Cambrian niches might have been more generalized than later niches (Valentine 1991 and references therein), with lax selection allowing greater amounts of variation within species and greater amounts of change between ancestor and descendant. Vacant ecospace might also have catalysed rapid amounts of change, with increasing incumbency (i.e. already filled niches) limiting possible morphological changes later in time. This would slow subsequent rates of morphological diversification and decrease average step-sizes even if intrinsic constraints remained unaffected. Postextinction radiations offer evidence of the effects of both incumbency and empty ecospace (e.g. the Cenozoic mammal radiation), as do radiations into new biogeographical regions (e.g. Darwin's finches).

Assessing and testing constraint hypotheses

Constraint hypotheses make predictions about: (1) intraspecific variation; (2) morphological disparity; and (3) step-sizes across phylogeny. Morphospace analyses, using either morphometric or discrete character data, can quantify intraspecific variation and disparity. Phylogenies can be modelled using a number of different approaches and, combined with morphospace analyses, permit the quantification of step-sizes.

Morphometric data and standard statistical tests can reveal significant differences in intraspecific variation among groups, either over time or across ecosystems. Although these data alone can demonstrate an increase or decrease in constraints, they cannot reject intrinsic or extrinsic hypotheses in particular. However, a general increase in intrinsic constraints predicts increasing constraint regardless of environment type, whereas a general increase in extrinsic constraints predicts that constraints should remain low in 'primitive' ecosystems. Thus, distinguishing the predictions of intrinsic and extrinsic constraint hypotheses might be possible when environmental controls are considered. For example, post-Cambrian trilobite species exhibit much less intraspecific variation than do Cambrian trilobite species, which suggests increased constraints (see Hughes and Chapman 1995 and references therein). However, Silurian trilobites from Cambrian-like palaeoenvironments display high intraspecific variation more typical of Cambrian species than of other post-Cambrian ones. None the less, these labile Silurian species appear to be related more closely to constrained Silurian taxa than to variable Cambrian species, which strongly suggests an extrinsic environmental control on morphological variation among trilobites.

Morphological disparity (i.e. the typical distance among taxa within a common morphospace) offers another way to examine constraint hypotheses. Morphological disparity that increases consistently against net diversification suggests that the distribution of step-sizes remained fairly constant in a clade's history (Foote 1996 and references therein) (Fig. 2.2.2.1a). Rapid increases in disparity at low taxonomic diversity, followed by plateaus or more gradual increases in disparity, suggest either a decrease in step-size (Fig. 2.2.2.1b) or a finite character space. Step-size changes and exhaustion of character space predict slightly different patterns. Decreased step-size without exhaustion predicts that morphological disparity should increase gradually within subclades, with little overlap among clades in morphospace. Exhaustion with no change in step-size predicts rapid increases in disparity within subclades, with disparity decreasing as increasing proportions of possible combinations of character states are realized.

If rapid increases in morphological disparity early in

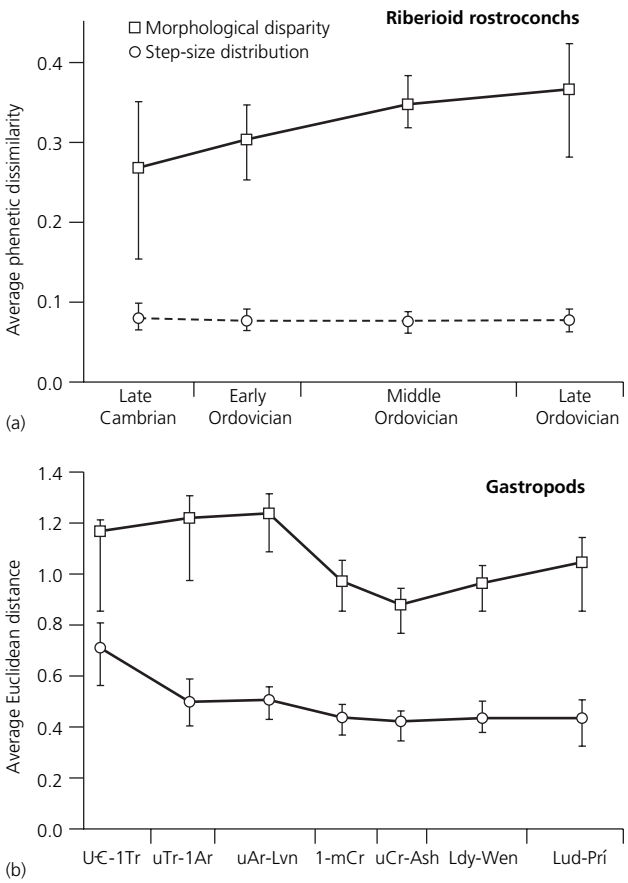

Fig. 2.2.2.1 Associations between step-size and morphological disparity. (a) No trend in step-size, yielding continuously increasing disparity. (b) Decrease in step-size over time, yielding an early peak in disparity. Error bars for disparity based on 100 bootstrap replications. Error bars for step-size represent 95th percentile zones.

clade histories are best attributed to high step-size, then the problem remains of distinguishing between intrinsic and extrinsic constraints. Intrinsic and extrinsic constraint hypotheses predict different patterns over subsequent events, such as near extinction followed by rebounds. Rapid increases in disparity early in rebounds (while diversity is still low) suggest elevated step-sizes. Because there is no reason to assume that intrinsic constraints changed over an extinction, the pattern is best explained as a response to the lifting of extrinsic constraints (i.e. the clearing of ecospace). Conversely, slow increases in morphological disparity under the same circumstances indicate low step-sizes, which suggest that intrinsic constraints increased early in clade evolution. Note that the second interpretation is valid only if there is no change in the ecological potential of a clade.

Patterns of morphological disparity can suggest constraints, but it is difficult to assess whether disparity patterns deviate significantly from the predictions of particular hypotheses. The assumptions of many apparently appropriate probability tests are violated because the points in morphospaces are not independent (due to phylogenetic autocorrelation). However, Monte Carlo (simulated) distributions using different models of morphological evolution, but maintaining observed information about taxonomic diversities and sampling intensities, offer the potential to assess the probability of particular hypotheses (see Foote 1996).

There has been debate about which dissimilarity metrics should be used in morphospace analyses: phenetic dissimilarity (i.e. net dissimilarities/comparable characters) or patristic (phylogenetic) dissimilarity (i.e. net dissimilarities+homoplastic similarities/comparable characters). Homoplastic similarities (i.e. convergences and parallelisms) might be acquired at any time, and will rapidly accumulate where there are finite possible character states. When testing for constraints, phenetic dissimilarity is appropriate because patristic dissimilarity cannot recognize limitations to possible character states and possible morphospace size. Even with molecular data, patristic dissimilarity cannot recognize that character spaces might be finite because each rederivation of, for example, adenine or guanine, is considered a unique condition. Thus, patristic morphospaces always portray morphospaces as continuously expanding.

Although patristic measures of disparity are not useful for examining constraints, integrating morphospace and phylogenetic analyses can be extremely insightful. Integrated analyses offer a direct assessment of step-size hypotheses, whereas morphological disparity alone offers only indirect assessments. Step-sizes are independent units; therefore, standard probability can identify significant differences in the distribution of step-sizes over time or across environmental gradients. Multiple shifts from one environment or trophic strategy to another, accompanied by similar shifts in step-size distributions, suggest that the ecologies provided different extrinsic constraints. Alternatively, intrinsic and extrinsic constraint hypotheses might predict changes in step-size for different suites of characters. Gastropods offer an example. Among modern gastropods, there is little association between internal anatomy (i.e. the 'slug') and basic ecological strategy. However, distantly related gastropods frequently share similar shell characters for ecological reasons. Thus, there is little evidence that intrinsic constraints limit functional shell characters or that clade-wide extrinsic constraints limit 'slug' characters. Fortunately, a few shell features reflect basic internal anatomy. Therefore, whereas increasing intrinsic constraints predicts reduced step-size over time for shell characters reflecting internal anatomy, increasing extrinsic constraints predicts reduced step-size over time for shell characters reflecting ecology and function. Although both patterns are observed, the pattern is much more significant for characters associated with internal anatomy than for characters associated with ecology. This result corroborates hypotheses of increased intrinsic constraints over time, at least in the case of gastropods (Wagner 1995).

The use of inferred phylogenies as models offers a test of ordered and finite state evolution hypotheses. Both hypotheses predict that the acquisition of new character states (the *y*-axis in Fig. 2.2.2.2) will slow down as changes accumulate (the *x*-axis in Fig. 2.2.2.2). This might be because only a fraction of states can be ancestral to new states (i.e. ordered evolution). Alternatively, there might simply be a finite number of plausible derived states. Simulated evolution, such as that shown in Fig. 2.2.2.2, indicates that the ordered states hypothesis predicts a slower decline in new state acquisition than does the finite states hypothesis. Phylogenies can also reveal suites of characters that evolve independently among some taxa, but which tend to appear in similar sequences in one portion of a phylogeny while evolving independently in other parts. This is consistent with changes in intrinsic constraints (i.e. developmental integration) for those characters.

Using inferred phylogenies as models to test constraint hypotheses offers several advantages over morphospace tests. However, many constraint hypotheses predict patterns that can obfuscate phylogenetic patterns. Most methods assume that shared derivations impart the same information about relationships throughout a phylogeny. This assumption is violated if characters change more frequently early or late in clade history (as predicted if constraints change over time) or if the character changes more frequently within one taxon than in another (as predicted if constraints vary among taxa). Second, limits on available characters

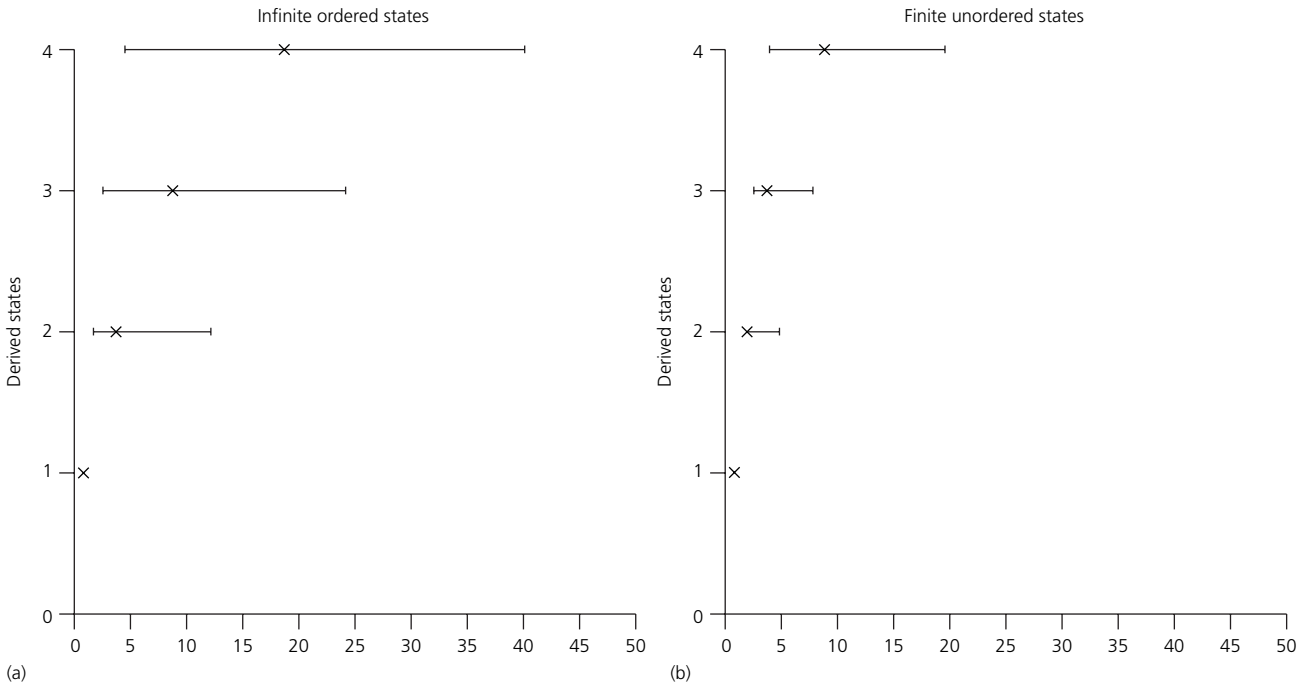

Fig. 2.2.2.2 The effects of (a) ordered series and (b) finite available characters on the evolution of new characters. Although both show decreases in the rates at which new characters are acquired, ordered characters yield power-series curves whereas finite states yield rarefaction-like curves. Ordered series based on averages from 100 simulations with 10 ordered characters with no boundaries on change. Finite states based on averages from 100 simulations with 40 unordered states over 10 characters. (Modified from Wagner 2000.)

mean that changes late in clade histories will recombine existing states rather than introduce new ones. Sampling now becomes very important to the accuracy of phylogenetic inference because combinations of characters possess more information about relationships than do particular morphologies. Finally, most phylogenetic methods must make assumptions about character orderings (of which, 'unordered' is simply one type of ordering). Incorrect assumptions might easily lead to incorrect phylogenies and thus unsound conclusions derived from that phylogeny. Numerous simulation studies demonstrate that all three aspects of constraints and changing constraints (varying rates over time and among taxa, limited or restricted state evolution, and incorrect assumptions about character state evolution) are sufficient to mislead phylogenetic methods such as minimum steps parsimony.

Conclusion

Palaeontological data can rarely address detailed hypotheses about constraint processes. However, palaeobiological studies can assess whether increasing or decreasing constraints are typical of clade evolution, whether changes in constraints were more common during particular intervals than others, and whether apparent changes in constraints are more common at particular phylogenetic levels. Thus, palaeobiological research that assesses these patterns and that attempts to delimit further the predictions of different constraint hypotheses is of great importance to general evolutionary theory.

References

Erwin, D.H. (1992) A preliminary classification of evolutionary radiations. *Historical Biology* **6**, 25–40.

Foote, M. (1996) Models of morphologic diversification. In: D. Jablonski, D.H. Erwin and J.H. Lipps, eds. *Evolutionary paleobiology: essays in honor of James W. Valentine*, pp. 62–86. University of Chicago Press, Chicago.

Foote, M. (1999) Morphological diversity in the evolutionary radiation of Paleozoic and Post-Paleozoic crinoids. *Paleobiology Memoirs*, Suppl. to *Paleobiology* **25** (2).

Hughes, N.C. and Chapman, R.E. (1995) Growth and variation in the Silurian proetide trilobite *Aulacopleura koninci* and its implications for trilobite palaeobiology. *Lethaia* **28**, 333–353.

Valentine, J.W. (1991) Major factors in the rapidity and extent of the metazoan radiation during the Proterozoic–Phanerozoic transition. In: A.M. Simonetta and S. Conway Morris, eds. *The early evolution of the Metazoa and the significance of problematic taxa*, pp. 11–13. Cambridge University Press, Cambridge.

Wagner, P.J. (1995) Testing evolutionary constraint hypotheses with early Paleozoic gastropods. *Paleobiology* **21**, 248–272.

Wagner, P.J. (2000) Exhaustion of cladistic character states among fossil taxa. *Evolution* **54**, 365–386.
Wright, S. (1978) *Evolution and the genetics of populations*, Vol. 4. *Variability within and among natural populations*. University of Chicago Press, Chicago.

2.2.3 Occupation of Morphospace

A.R.H. SWAN

Introduction: the morphospace concept

Morphospace is used to represent a range of morphological variation. Such a space may be expressed mathematically, drawn as a graph, or merely conceptualized. It is usually defined by perpendicular axes, one for each morphological attribute, and measurements of these attributes taken from a specimen allow it to be located in morphospace. Morphospace can provide a conceptual framework for any palaeontological investigation that involves morphology.

Consider two measurements taken from each of a number of fossil specimens, e.g. length and width of brachiopods; such data can be expressed in a bivariate scatter plot. The points on the plot can be regarded as actually occurring representatives of an infinite number of possible length/width combinations. Such a graph is a simple type of morphospace—a two-dimensional morphospace describing gross brachiopod shape. This framework can support both empirical investigations into the occupation of the space and theoretical studies into variations in functional properties across the space.

Parameter morphospace

Simple measurements such as length and width are often not sensitive to the process by which an organism constructs its form: an elongated gastropod shell may result from a high spire (e.g. *Turritella*) or from an elongate aperture (e.g. *Conus*). In many groups of organisms, parameters can be found which relate to the geometry of construction of the morphology and are consequently more efficient and powerful descriptors. The classic example is Raup's (1966) model for helicoid logarithmic spiral cone morphologies in molluscs and brachiopods based on four geometrical parameters (Fig. 2.2.3.1). Such

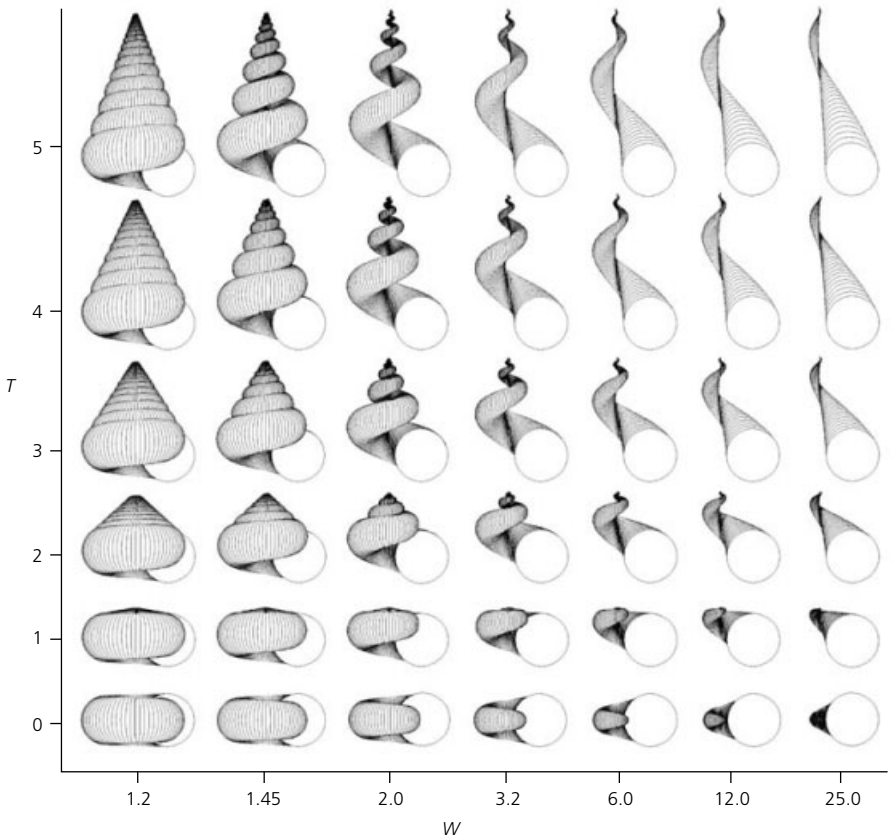

Fig. 2.2.3.1 A two-dimensional slice through Raup's (1966) *W-D-S-T* morphospace for helicoid log spiral cones. *W* is the whorl expansion rate, *T* is the whorl translation rate. The other parameters, *D*, the umbilical diameter as a proportion of the total diameter, and *S*, the whorl shape ratio, are constant at 0.1 and 1, respectively. Forms resembling gastropods occupy a band from top left to bottom centre, ammonites occur in the bottom left and brachiopods in the bottom right. Most bivalves have higher *W* than shown here.

geometrical models are the basis for the construction of very enlightening morphospaces, but it should be noted that the fit of geometric models to real morphologies is often only approximate.

Multivariate morphospace

The morphology of any organism can, in principle, be thoroughly quantified: if sufficient attributes are measured the resulting set of numerical values can be used to represent much of the information in a specimen (see Section 5.1.1). Useful morphospaces can be constructed by ordinating data against one, two, or three new axes which have directions in multidimensional space that are chosen so as to traverse the greatest range of variation in the dataset. The most popular method for achieving this is principal components analysis (PCA), where the new axes reflect intercorrelations among the attributes (Fig. 2.2.3.2; see also Fig. 5.1.3.1 for an application of a related technique). Such morphospaces incorporate an impressive amount of morphological information but have two disadvantages. Firstly, the axes are sample-dependent, being based on correlations between variables within the particular dataset used; other data could be plotted on the same axes but the representation of morphology would not be so efficient. Secondly, the locations in such a morphospace are not unique: different morphologies can plot at the same point (the differences being lost on reduction of dimensionality).

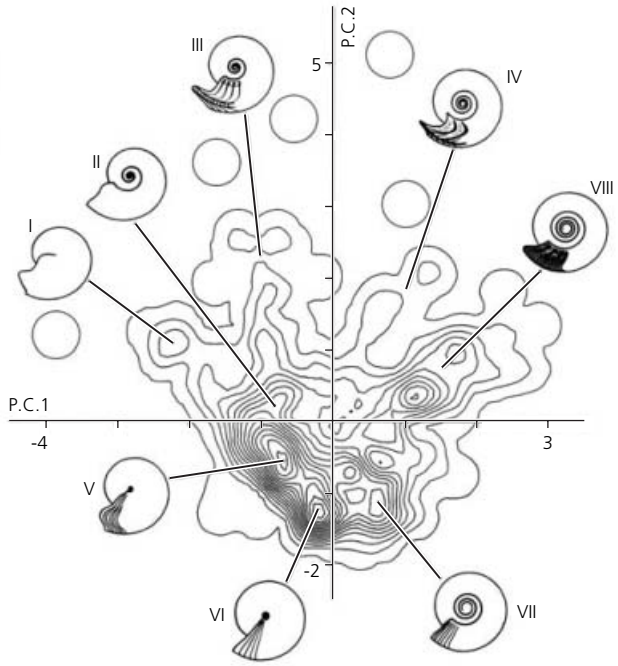

Fig. 2.2.3.2 Principal components plot of a 20-dimensional multivariate morphospace for Namurian ammonoids. The contours indicate the relative density of measured specimens. The occupation of morphospace is clearly heterogeneous, with a hand-shaped pattern. Eight morphotypes (I–VIII) are distinguished; representatives of each are shown. The morphotypes forming the 'fingers' (I, III, IV, and VIII) were adopted by various taxa through the Namurian, often derived independently from taxa having conservative morphology. (After Swan and Saunders 1987.)

Heterogeneities in morphospace

Morphospaces can encompass an infinity of possible morphologies (Richard Dawkins's 'museum of all shells') and computer programs can be used to generate any hypothetical morphology by user input of parameter values. Of key interest to palaeontologists, though, is the lack of homogeneity in the response of evolving organisms to the expanses of morphospace available to them.

Functional and fitness heterogeneity

It is clear that different parts of morphospace accommodate morphologies with different physical and functional properties. Morphologies from the array shown in Fig. 2.2.3.1 vary in structural strength and hydrodynamic response, and the apertural shapes shown in Fig. 2.2.3.3 vary in outline in a way that would affect deployment of musculature and feeding organs. These secondary properties can be quantified and plotted (see Swan and Saunders 1987), and regions of morphospace can be identified that should be favoured for certain modes of life: the distribution of evolutionary fitness can be investigated. A hypothetical colonial morphology with zooid apertures at branching nodes may be optimal when the zooids are uniformly distributed; an array of such morphologies is shown in Fig. 2.2.3.4(a) along with a plot of 'fitness', quantified using the nearest neighbour statistic (Fig. 2.2.3.4b). The complexity of the fitness heterogeneity is striking and is likely to be typical; a further example is the fitness, in terms of photosynthetic efficiency and mechanical strength, of branching structures in plants (Niklas and Kerchner 1984).

Occupation heterogeneity

Theoretical considerations show that morphologies are functionally different and it is no surprise that the distribution of actually observed morphologies is heterogeneous in morphospace. Some morphologies in Fig. 2.2.3.1 are clearly more frequent in nature than others,

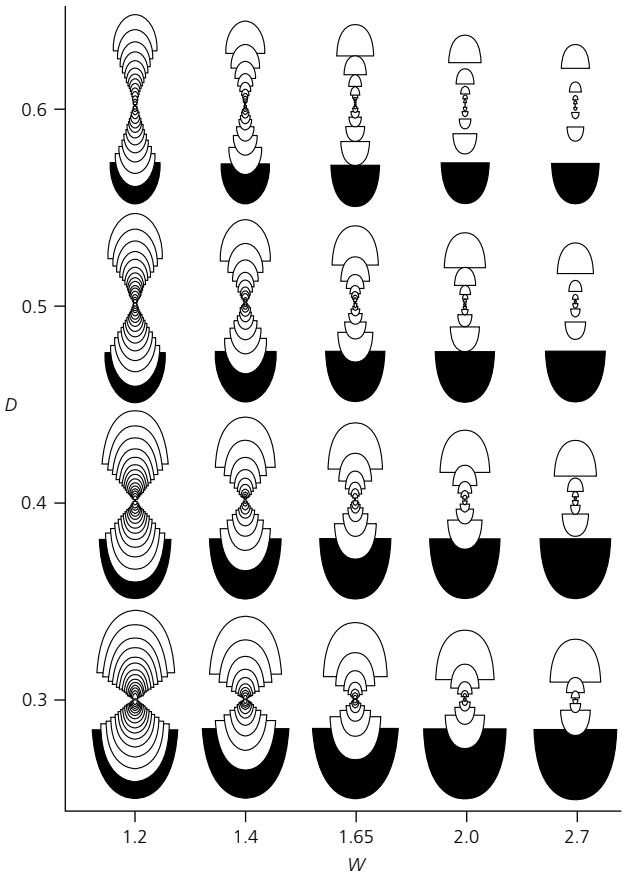

Fig. 2.2.3.3 *W-D* morphospace for ammonites and nautiloids shown in transverse cross-section (see Fig. 2.2.3.1 for definitions). The shaded whorl shapes represent the shape of the body in cross-section. Forms in the top right occur rarely: the loss of whorl-to-whorl contact when $W>1/D$ leads to structural weakness. Forms in the bottom left are also infrequent due to the extremely crescentic body shape.

and Fig. 2.2.3.2 shows a curious distribution of ammonoid specimens in a multivariate space. Heterogeneous distributions in parameter space can often be understood by comparison with functional properties, as is shown for ammonoid hydrostatics in Fig. 2.2.3.5. Insights may also be gained by plotting taxonomic subgroups (e.g. Fig. 5.1.3.1) or by the use of the time dimension (e.g. Dommergues *et al*. 1996).

Constraints imposed by bauplans

Raup's *W-D-S-T* morphospace (Fig. 2.2.3.1) contains fields that are characteristic of particular taxonomic groups (Raup 1966). This results from a number of geometric and functional constraints: bivalves and brachiopods need very high *W* to avoid the impairment of articulation that would result from prominent opposed

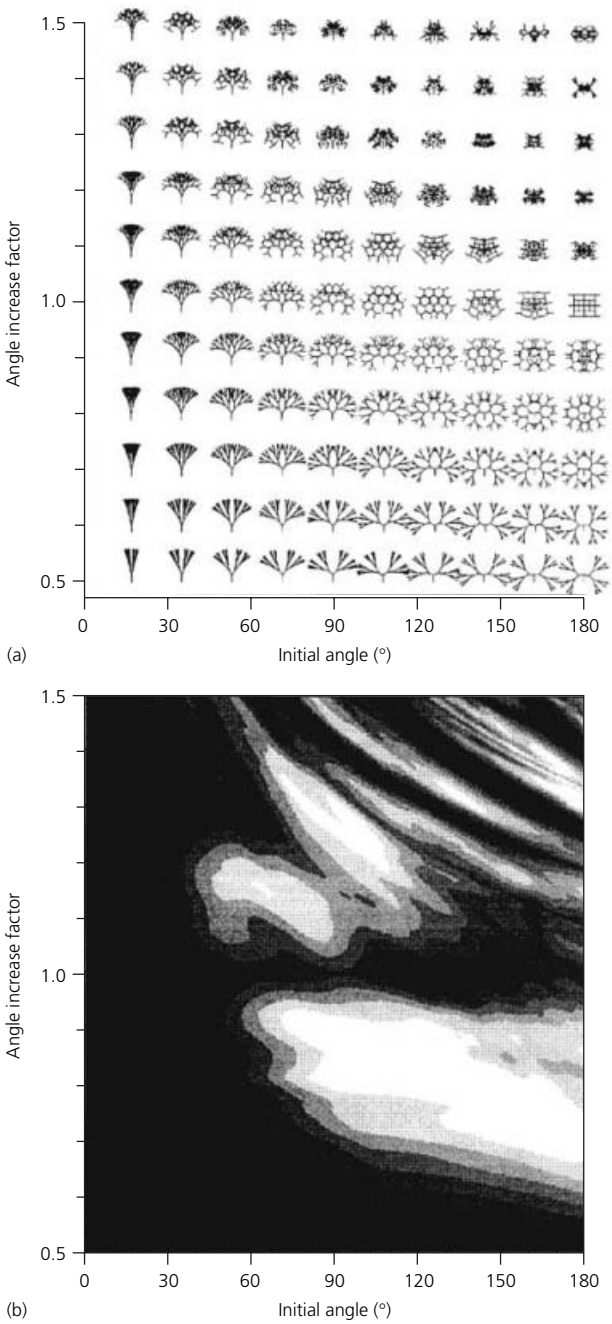

Fig. 2.2.3.4 A two-dimensional morphospace for dichotomously branching structures, defined by the angle of the first dichotomy and the factor by which this angle changes in each subsequent dichotomy. (a) Array of representative morphologies. (b) Fitness heterogeneity for the same space. The fitness measure is the nearest-neighbour statistic for hypothetical zooid apertures at branch nodes; paler shades indicate higher, more favourable, values (range: 0–1.7).

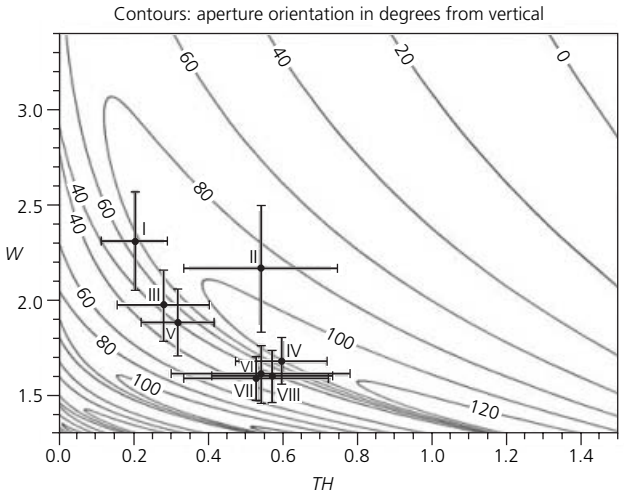

Fig. 2.2.3.5 A morphospace for planispiral ectocochliate cephalopods defined by *W* (see Fig. 2.2.3.1 for definition) and *TH*, a shell thickness parameter; these parameters are fundamentally important in determining hydrostatic properties. The contours show the calculated orientation of the animal in water, assuming neutral buoyancy. The centroids and standard deviation bars are shown for each of the eight Namurian ammonoid morphotypes shown in Fig. 2.2.3.2. Most morphotypes have positions in space corresponding to low aperture orientations, but morphotype II is shown to be anomalous. The correspondence between the data and the fitness heterogeneity helps to explain the morphology and validate the hydrostatic model. (After Swan and Saunders 1987.)

umbos; swimming ammonites need $T=0$ for bilateral symmetry; combinations of high *W*, *D*, and *T* lead to weak structures with no whorl-to-whorl contact. These considerations, though, apply globally and do not fully explain differences between the taxonomic groups; it is the inherited fundamental bauplan that separates the groups in morphospace. For example, brachiopods have $T=0$ because the valves are dorsal and ventral, unlike the left–right arrangement in bivalves. Less obviously, the characteristic buoyancy of the ectocochliate (externally shelled) cephalopods, enabled by the gas-filled phragmocone, constrains this group to low *W* so that there is sufficient volume in the phragmocone to compensate for the weight of shell and body. The gastropods have the least anatomical and functional constraints and hence the greatest morphological diversity.

Morphospace as a battleground

Various molluscan groups and brachiopods are constrained by their bauplans to occupy mutually exclusive regions of morphospace. Very often, however, two taxonomic groups in the same general habitat can and do develop similar morphology. Morphologies from different parts of morphospace are optimal for the occupation of different ecological niches (fitness maps such as Fig. 2.2.3.4 will change with every aspect of the local environment), so morphospace can be regarded as mapping on to ecological space. Consequently, competition for ecological resources can be represented as competition for regions of morphospace. Plots of Mesozoic ammonoids and nautiloids in *W-D* space suggest such a struggle (Ward 1980).

Taxonomy and phylogeny

Genetic and behavioural information is not normally available to palaeontologists, so taxonomic groups must be based on the morphology of fossils. Consequently, if a multivariate morphospace is defined which uses all relevant morphological attributes, then a species, genus, or higher taxon must occupy a discrete region of that space. However, this does not imply that a taxon can be recognized purely by analysis of the distribution of points in morphospace (perhaps by cluster analysis). Closeness in morphospace does not necessarily equate to relatedness; while some attributes are consistent, others may vary markedly within a taxon. Where two taxa evolve from different directions towards the same region of morphospace, convergence can be diagnosed. Convergence results from the commonality of specific functional adaptations and from the potential of taxa to 'customize' the inherited bauplan, and it suggests a degree of consistency in the environment. Morphotype III in Fig. 2.2.3.2, for example, was developed in response to recurring environmental conditions by three different ammonoid families in three different stages of the Namurian, all derived from morphotype V ancestors.

Conceptually, phylogeny is a tree in morphospace linking points that represent known specimens. The idea of a phylogenetic diagram with time and morphology as axes is appealing but, unfortunately, very large numbers of attributes usually need to be considered and morphological ordinates cannot be used in the construction of cladograms. Nevertheless, low-level taxonomic and phylogenetic problems can sometimes be resolved using morphospace plots. Furthermore, morphospace plots undertaken for functional morphological analysis may yield phylogenetic information. In the analysis of Carboniferous ammonoids shown in Fig. 2.2.3.5, all of the morphotypes I–VIII are occupied by a variety of goniatitid taxa except morphotype II, which is represented only by the prolecanitids (Order Agoniatitida). As well as reflecting differences in function, this characteristic position in *W-TH* space appears to be a previously unsuspected synapomorphy of the prolecanitids and their descendants, which include the ammonites.

Evolution as a walk in morphospace

With the benefit of hindsight, it is often easy to explain morphospace occupation in terms of functional optima, but the evolving population cannot 'see' these optima and only experiences selection pressure blindly and iteratively. Selection pressure corresponds to a vector in morphospace in a direction towards greater fitness: each generation takes a blind step 'uphill' on a topography that is not only complex (as in Fig. 2.2.3.4) but frequently changing. This leads to the deduction that occupation of optimal parts of morphospace is not guaranteed: evolution can lead to local, rather than global, optima. The history of adaptation of a species to changing environments determines its route through morphospace, and this can affect its success at attaining a global fitness summit (Niklas 1997). A species may have a simple route between successive positions of the fitness summit during environmental change (for example, in cases of preadaptation). Conversely, environmental change may isolate a species from the new fitness peak, and fortuitous 'hopeful monster'-type mutations may be needed to leap low-fitness valleys.

Towards a universal morphospace

It is possible to conceptualize a morphospace containing all possible organic forms. For palaeontological purposes, a 'skeleton space' can be defined, in which all actual and hypothetical skeletal elements may be located (Thomas and Reif 1993). Unlike the morphospaces discussed above, a universally applicable morphospace cannot be defined by a small number of parameters with continuous scales; instead, there are many attributes but each has a small number of discrete states, giving a large but finite set of permutations. For example, two attributes may be 'geometry' (including the states 'rods' and 'plates') and 'topology' (with states 'external' and 'internal'). The morphospace of these two attributes has four possible positions: external rods (e.g. echinoid spines), internal rods (e.g. limb bones), external plates (e.g. scales) and internal plates (e.g. skull bones). Initial compilations of skeletal elements from various organisms leads to the interesting conclusion that the universal morphospace is quite well filled by known organisms. An analysis of arthropod morphology using a similarly general method of coding attributes (Briggs *et al.* 1992; see also Section 5.1.3) demonstrates that occupation of morphospace in the Cambrian was as expansive as at present. Some hypothetical morphologies may remain unused due to fundamental and universal physical constraints, but life, through the mechanism of evolution, is remarkably efficient at exploring and occupying morphospace.

References

Briggs, D.E.G., Fortey, R.A. and Wills, M.A. (1992) Morphological disparity in the Cambrian. *Science* **256**, 1670–1673.

Dommergues, J.-L., Laurin, B. and Meister, C. (1996) Evolution of ammonoid morphospace during the Early Jurassic radiation. *Paleobiology* **22**, 219–240.

Niklas, K.J. (1997) Effects of hypothetical developmental barriers and abrupt environmental changes on adaptive walks in a computer-generated domain for early vascular land plants. *Paleobiology* **23**, 63–76.

Niklas, K.J. and Kerchner, V. (1984) Mechanical and photosynthetic constraints on the evolution of plant shape. *Paleobiology* **31**, 35–52.

Raup, D.M. (1966) Geometric analysis of shell coiling: general problems. *Journal of Paleontology* **40**, 1178–1190.

Swan, A.R.H. and Saunders, W.B. (1987) Function and shape in late-Paleozoic (mid-Carboniferous) ammonoids. *Paleobiology* **13**, 297–311.

Thomas, R.D.K. and Reif, W.-E. (1993) The skeleton space: a finite set of organic designs. *Evolution* **47**, 341–360.

Ward, P.D. (1980) Comparative shell shape distributions in Jurassic to Cretaceous ammonites and Jurassic to Tertiary nautilids. *Paleobiology* **6**, 32–43.

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2.3 Macroevolution

2.3.1 Origin of Evolutionary Novelties

D. JABLONSKI

Introduction

The term 'evolutionary novelty' might denote a change in any aspect of an organism from primitive to derived state, but for macroevolutionary purposes an evolutionary novelty usually involves a dramatic shift in form or behaviour, often a shift that significantly alters the function or the ecological role of an organism. This remains a loosely defined concept that has been applied inconsistently and at many levels (see Jablonski and Bottjer 1990 and Müller and Wagner 1991 for reviews). Thus, wings in insects, birds, and bats can be treated as novelties, but so can each of the components, such as the musculature, feathers, or membranes, of the flight apparatus.

A related concept is *key innovation*, which, although sometimes used as a synonym for evolutionary novelty, often denotes the particular subset of novelties that triggered major evolutionary diversifications. The hypothesis that a particular novelty was the direct cause of a diversification is difficult to test rigorously: each well-defined group will be characterized by one or more derived characters, so that any group-defining character might retrospectively seem to have been the critical trigger for all subsequent diversification, even when that character was not the crucial factor (but see below for a combined functional and phylogenetic approach to this problem). The difficulties in testing the role of key innovations aside, it is useful to note that many striking evolutionary novelties did not result in prolific diversifications and thus are not key innovations in the usual sense, so that the terms cannot be treated interchangeably. Consider anteaters, for example: a lineage with distinct adaptations that has apparently included only a few species at any one time.

The fossil record provides a unique perspective on the origin and consequences of evolutionary novelties, by permitting a direct assessment of the timing, context, and subsequent behaviour of a given clade and its associated biota. Evolutionary novelties are the raw material of evolution, sorted and moulded by selection and other forces (see Section 2.3.6), and palaeontological data are a key element in assessing the patterns and processes underlying the origin and fate of these raw materials.

Patterns

One of the most important contributions that palaeontology makes to evolutionary theory is the recognition that novelties have not arisen randomly in time and space. The temporal pattern is particularly striking for marine organisms: the first occurrences of major evolutionary novelties are concentrated near the beginning of the Palaeozoic Era, in what has been termed the 'Cambrian explosion', and, in less dramatic fashion, in the intervals following mass extinctions. This early Palaeozoic pulse was recognized first by tallies of the first fossil occurrences of animal phyla and classes, and more recently by analyses that directly quantified morphological variety, independent of taxonomic or phylogenetic data (see Foote 1997 for review, and Section 5.1.3). Although considerable controversy remains about the timing of the deeper phylogenetic branchpoints that eventually led to the modern phyla, this does not negate the significance of the flood of evolutionary novelties that appeared in the early Palaeozoic (Valentine *et al.* 1999) (see Section 1.2.1).

The early expansion of morphological diversity is not matched by diversity patterns at low taxonomic levels (family, genus, or species), and does not continue unabated—although more modest pulses of novelty production do occur in the wake of mass extinctions, particularly the huge Permo-Triassic event. The reasons for this temporal pattern are controversial; the opposing hypotheses might be termed 'extrinsic' and 'intrinsic'. Extrinsic factors are ecological: the Cambrian explosion represents the opportunistic invasion of unexploited ecological niches; as those niches became more fully occupied and ecological interactions intensified accordingly, fewer opportunities would have been open for highly divergent evolutionary novelties to become established. Species might continue to proliferate, but as variations upon the major morphological themes that were set early in the diversification. The lesser pulses after mass extinctions represent a partial clearing of ecospace and a commensurate interval of successful evolutionary creativity. In contrast, intrinsic factors are genomic: the Cambrian explosion represents a time when developmental systems were more loosely organized, regulated, or canalized. As those systems evolved to a configuration more like today's highly buffered and

redundant systems, highly divergent novelties were less likely to arise.

In theory, the extrinsic and intrinsic hypotheses contrast starkly. One postulates a constant rate of novelty production, with palaeontological patterns modulated by the availability of ecological opportunities for those novelties to exploit, while the other postulates a genetically driven decline in the rate of novelty production itself. However, without a time machine to perform and monitor reciprocal transplant experiments between Cambrian and modern seas, these alternatives have been extremely difficult to test. The extrinsic hypothesis appears to be slightly preferred at the moment, for two principal reasons. First, the accelerated rates of novelty production seen after mass extinctions, and with the invasion of new habitats (e.g. the rapid acquisition of novelties in the early diversification of land plants; see Section 1.3.4), suggest an ecological control subject to rejuvenation. Second, most of the elements of one important developmental system, the *Hox* genes that help to specify segment identity along the body axis, appear to have been in place prior to the Cambrian explosion. However, given how little is known about the workings of early developmental systems, and particularly about their evolutionary assembly, this judgement may be premature.

Not all novelty production is tied to the Cambrian explosion or to mass extinctions, especially at lower levels. For example, the rate and pattern of novelty production within the marine bryozoan orders during the Mesozoic is more closely related to the diversification rate of each order than to proximity to mass extinction events. The slowly diversifying cyclostomes survive the great Permo-Triassic extinction but show no postextinction pulse in novelty production, whereas the rapidly diversifying cheilostomes capture novelties in rapid succession during the Early Cretaceous (see Fig. 2.3.1.1) at some remove from major extinction events (Jablonski *et al.* 1997). Comparative analyses of rates of novelty production among clades with strongly differing origination rates at the species and genus level would shed valuable light on the relative roles of intrinsic and extrinsic factors away from major perturbations.

Spatial patterns are more poorly known, but for marine invertebrates major evolutionary novelties appear to originate preferentially in nearshore, disturbed habitats. As in the temporal pattern, this observation appears to hold for both taxonomic and morphological data, and contrasts significantly with patterns shown for minor novelties within the major groups (Jablonski and Bottjer 1990; Jablonski *et al.* 1997) (Fig. 2.3.1.1). Similar patterns occur in Palaeozoic and post-Palaeozoic land plants (e.g. DiMichele and Aronson 1992). As with the temporal patterns, both intrinsic and extrinsic explanations have been offered, from the genetics of populations isolated in nearshore patchy habitats, to hypothesized bathymetric gradients in niche availability owing to local extinction and recolonization.

Palaeontological data have also been brought to bear on the long-standing question of whether the tropics are a cradle or a museum of evolutionary novelty. Such analyses are complicated by the greater intensity of study and collection of fossils in today's northern mid-latitudes, which would probably skew any simple biogeographical mapping of first appearances. However, when these sampling biases are factored out of the marine invertebrate record (for example, by comparing the first appearances of orders to the latitudinal distribution of species-level records), the tropics appear to be a source of evolutionary novelty in post-Palaeozoic time (Jablonski 1993). As with the temporal and environmental patterns discussed above, latitudinal patterns at high taxonomic levels are not simple extensions of those seen at lower levels: species and genera, in contrast to orders, are evidently as likely to originate at high latitudes and expand equatorward as the reverse.

This pervasive phenomenon of discordance across hierarchical levels, where the deployment of major evolutionary novelties in time and space is not simply a function of species-level processes, suggests an evolutionary dynamic that operates at several semi-independent levels. In any event, the fossil record shows just how strong a stamp ecological, and perhaps developmental, factors place on the major features of evolution (see Jablonski 2000).

Impact of novelties

The consequences of evolutionary novelties are highly variable. On the one hand, the acquisition of evolutionary novelty can limit future evolutionary directions (e.g. Müller and Wagner 1991); the morphological commitment to flight in bats severely limits their mobility on the ground, for example (see Section 2.2.2). On the other hand, many novelties are viewed as adaptive breakthroughs that initiated prolific diversifications, although as noted above many dramatic novelties do not trigger such diversifications and, conversely, many diversifications are difficult to link rigorously with a particular novelty. Even when novelties have undoubted adaptive value, their acquisition may not have been sufficient to drive a diversification. For example, the suite of mammalian characteristics, including homeothermy, live birth, and milk production, were evidently in place long before the extinction of the dinosaurs and other Mesozoic dominants opened opportunities for the great mammal radiations of the Cenozoic (see Section 1.3.10). Combined functional and phylogenetic approaches, most powerfully applied when novelties have evolved convergently multiple

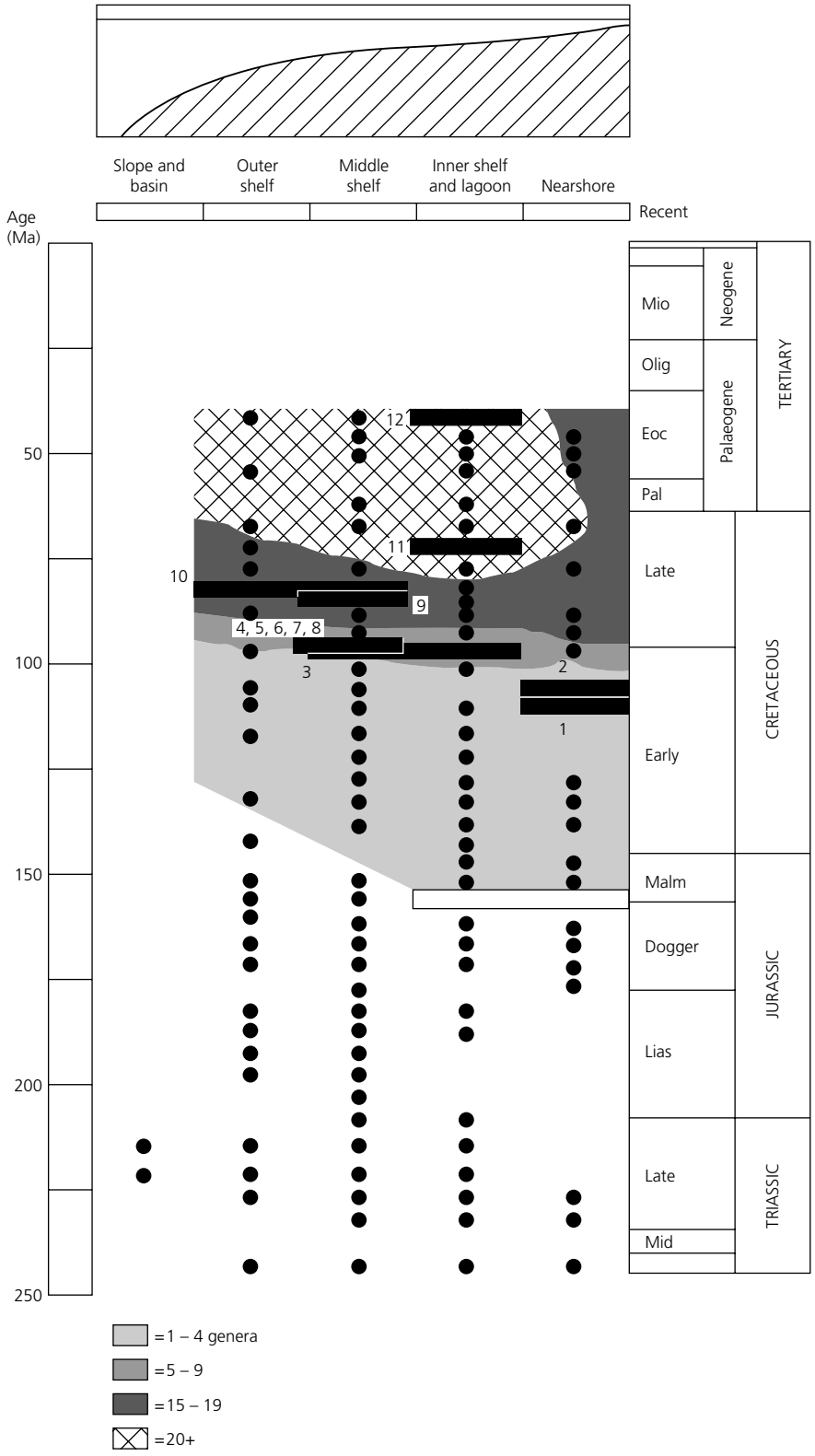

Fig. 2.3.1.1 Environmental patterns in the origin of evolutionary novelties in cheilostome bryzoans. Like many post-Palaeozoic orders, the group originated onshore (open bar), but the within-group novelties (solid bars with numbers) are evenly distributed across the continental shelf. In analyses of environmental histories, absences of a target group must be assessed for their reliability before they can be used to define distributional shifts through time. Here, points outside the shaded contours represent taphonomic control points—locations where another group has similar preservational characteristics (in this case cyclostome bryozoans)—that support absences of the target group. (From Jablonski *et al.* 1997, with permission.)

times so that their association with diversifications can be tested statistically, are being applied to living and fossil groups as a means of testing hypotheses of key innovations (Sanderson and Donoghue 1996; Hunter 1998).

Not all diversifications need be a direct consequence of advantages conferred by a novel adaptation: evolutionary changes that yield increased speciation rates (e.g. the acquisition in marine invertebrates of a low-dispersal larval type) could be an indirect cause of increased species richness in a clade. Such indirect effects have been proposed for molluscs, bryozoans, various insect groups, and flowering plants.

Evolutionary novelties do not arise in an ecological vacuum, and so may affect other taxa. Definitively tracing the impact of specific characters or taxa on their biotic milieu is difficult, but some large-scale patterns have been proposed. The acquisition of novel adaptations for penetrating hard-shelled prey by crustaceans, seastars, teleost fishes, and certain gastropods evidently had a significant impact on the morphology of their targets during the late Mesozoic and Cenozoic, although the evolutionary dynamics of the response were highly varied (see Section 1.4.1). In a more benign example, the suite of novelties that enabled plants to invade the land established the base of a terrestrial food chain that allowed animals to follow and diversify (see Section 1.3.6).

Generation of novelties

The study of evolutionary novelty has entered a new phase with major strides in understanding the structure and regulation of the developmental programmes that underlie morphological features. The origin of novelty was once viewed almost exclusively in terms of the operation of many genes of equally small effect. While such genes are undeniably central to the evolutionary response of populations to natural selection and other forces, a number of workers have begun to explore the roles of the sets of genes, such as *Hox* genes, that themselves regulate the timing and location of gene expression during the development and growth of an organism. Because gene interactions involve complex networks, the old structural vs. regulatory gene dichotomy is difficult to maintain, but multiple sets of gene signalling pathways, in which a relatively few control genes modulate the expression of batteries of many downstream genes, are important components of genome organization. The dissection of developmental processes at the molecular and cellular level is proceeding at a remarkable pace (see Jablonski 2000 and Section 2.2.1).

Characters and functional evolution

Two key aspects of developmental biology for the origin of evolutionary novelty are integration and modularity. Development is orchestrated by a hierarchy of genes, and by cell interactions in the developing embryo that integrate the differentiating regions (which can behave in modular fashion) into a functional organism. This means that at least some evolutionary novelties can be accommodated by coordinated changes that need not require independent genetic events. A host of laboratory experiments indicate that enlargement of an eye or elongation or reorientation of a limb bone, for example, can evoke a set of developmental responses, such as increased production of blood vessels, nerves, and even remodelling of bone and muscle, that can (within limits) combine to produce a still functional organism, simply by drawing on the integrative machinery of the developmental system (see Hall 1998). (The claim that evolutionary novelties can sometimes evolve in coordinated fashion, mediated by developmental mechanisms, does not require that novelties arise abruptly and discontinuously on the short time scales studied by experimental biologists. Severe limits, still poorly understood, clearly exist on the kinds of evolutionary changes that can be achieved or accommodated developmentally.)

At the same time, because the embryo is modular, with genetically discrete subunits, accommodations in one part need not extend throughout the body; the novel limb morphology need not disrupt, for example, skull development. These developmental modules can themselves evolve and even break apart, so that formerly linked and covarying aspects of morphology can become dissociated (see Raff 1996; Wagner 1996). This dissociation is the developmental basis for the pervasive phenomenon of mosaic evolution, in which derived features coexist with primitive ones, juxtaposing the wings and feathers of *Archaeopteryx* with its dinosaurian jaws, pelvis, and tail, or the small braincase of early hominids with their upright posture.

The evolutionary pathways of developmentally important genes and their roles—that is, the genetic underpinnings of evolutionary novelty—are proving to be no less complex than any other aspect of the biology of organisms. Many of the genes that control development are remarkably conserved across the animal kingdom, from anemones to vertebrates, but this is no guarantee that those genes have always performed the same developmental tasks. For example, the genetic machinery that patterns the limbs of arthropods and vertebrates is similar, but primitive chordates (and probably a worm-like common ancestor) lack paired limbs; thus a simple assumption of conserved gene function and derivation of the arthropod and vertebrate limb from a common ancestral appendage is untenable (Shubin *et al.*

1997). One lesson that applies across the biological hierarchy, from molecules to bodies, is that evolution almost always proceeds by tinkering, i.e. by modifying old structures and pathways for new functions, rather than by fabricating complex new features all at once. Thus, the bony structures of limbs evolved to support fish fins and their regulatory genes evolved in support of much simpler patterning tasks perpendicular to the body axis. Such features, coopted for uses unrelated to their origins, are termed 'exaptations' and have become a focus for multidisciplinary study. More generally, it is becoming increasingly clear that the fullest understanding of evolutionary events leading to major novelties will require an interdisciplinary partnership, integrating developmental and palaeontological data within a phylogenetic framework (Shubin *et al*. 1997; Valentine *et al*. 1999).

References

DiMichele, W.A. and Aronson, R.B. (1992) The Pennsylvanian–Permian vegetational transition: a terrestrial analogue of the onshore–offshore hypothesis. *Evolution* **46**, 807–824.

Foote, M. (1997) The evolution of morphological diversity. *Annual Review of Ecology and Systematics* **28**, 129–152.

Hall, B.K. (1998) *Evolutionary developmental biology*, 2nd edn. Kluwer, Dordrecht.

Hunter, J.P. (1998) Key innovations and the ecology of macroevolution. *Trends in Ecology and Evolution* **13**, 31–36, 281–282.

Jablonski, D. (1993) The tropics as a source of evolutionary novelty: the post-Palaeozoic fossil record of marine invertebrates. *Nature* **364**, 142–144.

Jablonski, D. (2000) Micro- and macroevolution: scale and hierarchy in evolutionary biology and paleobiology. In: D.H. Erwin and S.L. Wing, eds. *Deep time: paleobiology's perspective*, pp. 15–52. *Paleobiology* **26**, (suppl. to no. 4).

Jablonski, D. and Bottjer, D.J. (1990) The ecology of evolutionary innovations: the fossil record. In: M.H. Nitecki, ed. *Evolutionary innovations*, pp. 253–288. University of Chicago Press, Chicago.

Jablonski, D., Lidgard, S. and Taylor, P.D. (1997) Comparative ecology of bryozoan radiations: origin of novelties in cyclostomes and cheilostomes. *Palaios* **12**, 505–523.

Müller, G.B. and Wagner, G.P. (1991) Novelty in evolution: restructuring the concept. *Annual Review of Ecology and Systematics* **22**, 229–256.

Raff, R.A. (1996) *The shape of life: genes, development, and the evolution of animal form*. University of Chicago Press, Chicago.

Sanderson, M.J. and Donoghue, M.J. (1996) Reconstructing shifts in diversification rates on phylogenetic trees. *Trends in Ecology and Evolution* **11**, 15–20.

Shubin, N., Tabin, C. and Carroll, S. (1997) Fossils, genes and the evolution of animal limbs. *Nature* **388**, 639–648.

Valentine, J.W., Jablonski, D. and Erwin, D.H. (1999) Fossils, molecules and embryos: new perspectives on the Cambrian explosion. *Development* **126**, 851–859.

Wagner, G.P. (1996) Homologues, natural kinds and the evolution of modularity. *American Zoologist* **36**, 36–43.

2.3.2 Controls on Rates of Evolution

S.M. STANLEY

Introduction

Rates of evolution vary greatly among taxa, and they also vary within taxa in space and time. Inherent traits of taxa influence rates of evolution, as do both biotic and abiotic aspects of the environment. Rates of evolution can be measured by either taxonomic or morphological metrics, and these two kinds of metrics provide different opportunities for analysing factors that govern the pace of evolution.

Taxonomic rates

Either species or higher taxa can serve as units for measuring taxonomic rates. Species provide better resolution, but the incompleteness of the fossil record commonly dictates the use of higher taxa as units; the record of higher taxa is usually more complete than that of species because the fossil occurrence of even a small fraction of the species belonging to a higher taxon can approximately document the higher taxon's stratigraphic range.

Taxonomic rates amount to branching rates for taxa (speciation rates in the case of species), which means that they are inherently exponential, rather than arithmetic, in nature. In other words they are appropriately calculated as fractional additions of taxa per unit time rather than as mere numbers of new taxa per unit time. For the early stage of an evolutionary radiation, the net rate of increase in number of species can be taken to be approximately exponential (Fig. 2.3.2.1a) (Stanley 1979):

$$N = N_0 e^{Rt}$$

where R is the net rate, N_0 is the original number of species (1 in the case of radiation from a monophyletic origin), N is the number of species at the end of the time interval considered (t), and e is the base of natural logarithms.

The rate (R) is actually a net rate, equalling rate of speciation (S) minus rate of extinction (E), just as net rate of increase for money in a bank equals rate of interest minus rate of withdrawal:

$$R = S - E$$

Rate of extinction (E) is the reciprocal of mean species longevity, which can be measured or estimated from fossil data. Adding this value to R for a given adaptive radiation gives rate of speciation (S). Occasionally the fossil record is of such high quality that N can be tallied

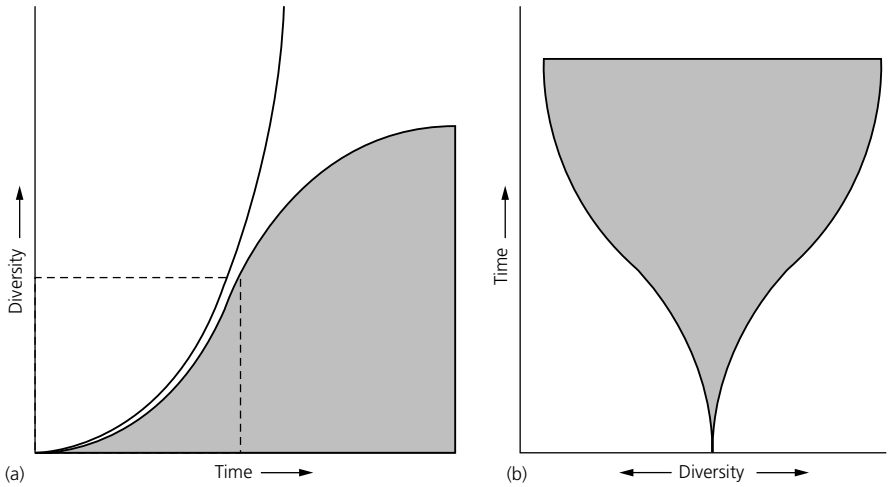

Fig. 2.3.2.1 Graphic portrayal of unbridled and damped exponential diversification. (a) The convex upward curve illustrates purely exponential increase. The sigmoid curve bounding the shaded area represents damped exponential increase, in which the fractional rate of increase declines as diversity increases. In the early stage of radiation (for example, the stage represented by the portion of the graph between the origin and dashed lines), there is little separation between the two curves. (b) The shaded portion of (a) rotated 90° and replotted symmetrically about a vertical axis to form a balloon diagram of the sort commonly used to depict taxonomic diversity through time. (From Stanley 1979.)

accurately for a given past time, but N is more readily tallied for the present, for a taxon currently at an early stage of adaptive radiation.

Rate of branching can also be calculated for a taxon that is not in the midst of adaptive radiation as a per-taxon addition of daughter taxa per unit time.

Morphological rates

Haldane proposed the darwin as a unit for quantifying rates of morphological change in evolution. This is the rate of change by a factor of e, the base of natural logarithms, per million years. The rate in darwins equals $\ln x_2 - \ln x_1/t$, where x_1 and x_2 are the initial and final character states. A change of 2.7% per million years represents 10 millidarwins. A comparable metric, which has the advantage of producing numbers whose significance is easier to visualize than the darwin, is simply the fractional change per unit time for a morphometric variable (Stanley and Yang 1987). The mean rate for several variables can be calculated to depict the pace of evolution more comprehensively. Mean rate of change for one or more morphometric variables can be calculated for a clade, rather than a single lineage, but such a rate is of limited value without information as to how the change was partitioned between cladogenesis (speciation) and anagenesis (evolution within an unbranching lineage, sometimes termed 'phyletic evolution'). Furthermore, most shifts in mean value for a morphometric variable within a clade entail not only evolution but also extinction. In fact, differential rates of extinction alone can produce a net morphological trend within a clade.

Most published morphological rates of evolution ostensibly represent anagenesis. For relatively few of these rates, however, have the end-member populations been convincingly demonstrated to belong to a single lineage (an unbranched line of descent). Furthermore, the vast majority of these published rates depict nothing more than change in body size (Stanley and Yang 1987).

Net rates of anagenesis lose significance if actual rates varied markedly during the interval considered. For the extreme situation, in which virtually all change was concentrated within one or more very short subintervals, the net rate of anagenesis is virtually meaningless; this pattern can be termed 'staircase evolution', and the very high rates for the short subintervals warrant measurement and interpretation.

Whereas, in accordance with Dollo's Law, a morphologically complex evolutionary trend is unlikely to be reversed, evolutionary reversal for a single variable is not uncommon. Multiple reversals create a zigzag pattern without necessarily producing an appreciable amount of net evolution. Such a pattern can give problematical results. Typically, the measured rate of phyletic evolution decreases with the length of the interval considered (Fig. 2.3.2.2).

No trait remains absolutely fixed over the course of even a few generations. Since some degree of change is inevitable, an appropriate yardstick is required to allow the significance of any measured change or calculated rate to be evaluated. One study of change within extant lineages of bivalve molluscs compared multivariate morphological differences between 4-myr-old populations to comparable differences among geographically

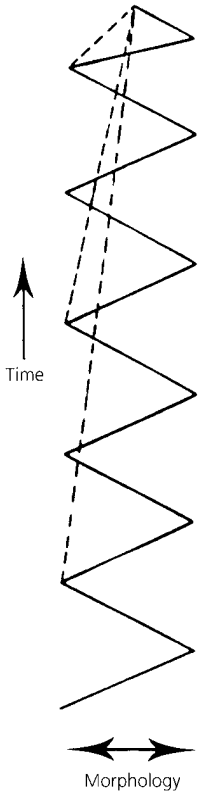

Fig. 2.3.2.2 Diagram illustrating how a zigzag pattern of anagenesis yields lower maximum measured net rates of evolution as the interval for which the rates are measured increases. (From Stanley and Yang 1987.)

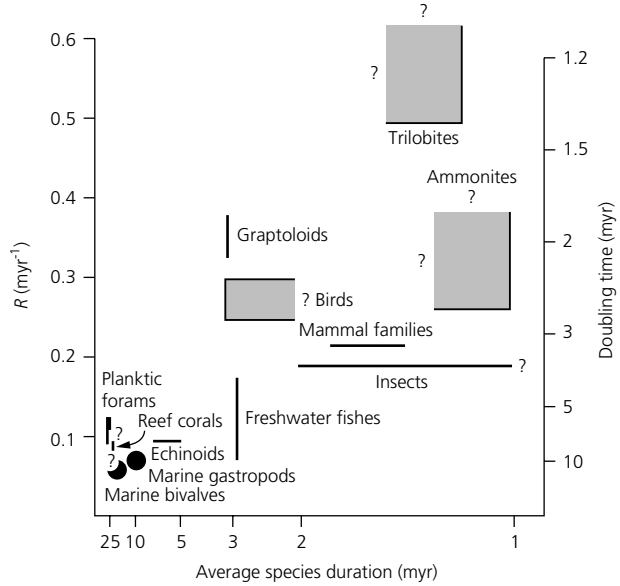

Fig. 2.3.2.3 Plot showing how, for a variety of animal taxa, rate of speciation in adaptive radiation is correlated with rate of extinction. Mean rate of extinction (E) is the inverse of mean species duration. Average species duration is plotted on an inverse scale, as a surrogate for E, because it is not a precise mean and because pseudo-extinction has not been factored out; thus, the position of a group along the horizontal axis is only a rough estimate of mean rate of extinction. R is the measured rate of exponential increase in number of species for a sizeable taxon early in adaptive radiation; this is plotted as a surrogate for rate of speciation because the latter (S) equals R plus E (there is an auto-correlation between S and E). Even though numbers on the graph are not precise, there are such great differences between taxa with high rates and taxa with low rates that the trend of the plotted data must be generally accurate. Small pulses of radiation (ones yielding only a few species) can occur within various taxa at higher values of R than are shown here; the rates plotted represent radiations that have yielded dozens of species. (From Stanley 1979.)

separate populations of the same or a very similar living species (Stanley and Yang 1987). About 90% of the differences between the fossil and living populations fell within the range of differences between geographically separated extant populations; despite a bit of morphological zigzagging, there was very little net evolution. In another approach, variances for rates of multivariate change within species (lineages) of bryozoans during brief intervals of Neogene time were compared to equivalent variances for rates between species (Cheetham 1986) (see Section 2.1.2). The question was whether evolutionary trajectories for anagenetic trends could yield new species that appeared within the clade under investigation (see Fig. 2.1.2.1). The answer was that they could not. In fact, anagenetic rates were not significantly different from zero (Fig. 2.3.2.3). Both these studies of anagenetic change supported the punctuational model of evolution, which attributes most evolution to speciation events rather than to anagenesis.

The advent of the punctuational model of evolution (Eldredge and Gould 1972) focused attention on the locus of evolutionary change. The evidence that approximate evolutionary stasis for species over millions of years is very common (Stanley 1979) indicates that anagenetic rates are frequently so small as to be virtually insignificant. According to this model, geologically long-ranging clades that always include very few species should automatically experience very low net rates of morphological evolution because such clades experience very few speciation events. In fact, living representatives of extant clades of this kind seem invariably to constitute 'living fossils': forms that differ little from the earliest members of their clades.

The common occurrence of approximate evolutionary stasis raises the question: What prevents species from evolving appreciably over millions of years? R.A. Fisher's classic fundamental theorem of natural selection states that rate of evolution should increase with the genotypic variance within a population. What, then, pre-

vents natural selection from acting on the substantial genotypic variance that is generally present within species, to produce substantial change? Some workers have argued that stabilizing selection, governed by extrinsic factors, is at work. Others have attributed a larger role to morphogenetic constraints. In fact, the two forms of control are not mutually exclusive. Morphogenetic constraints are not absolute. Freakish features that violate normal morphogenetic constraints appear in populations but are nearly always selected against, and the weeding out of such features represents stabilizing selection.

It is difficult to identify the selection pressures that have produced observed anagenetic trends whose rates can be measured. The phylogeny of Neogene horses (Hulbert 1993) is an exception, appearing to display polyphyletic anagenetic trends toward taller molar teeth that can be explained as a response to protracted environmental change. These anagenetic trends for molars parallel net trends that result from: (1) higher rates of speciation for species with relatively tall molars; and (2) a tendency for speciation events to produce daughter species with taller teeth than their parent species. The environmental factor favouring all of these changes was the spread of grasslands, which provided fodder that was highly abrasive, favouring animals with relatively tall teeth that could tolerate substantial wear.

Intrinsic biological features that influence rates of speciation

Several inherent traits of organisms contribute to variability among taxa in mean rate of speciation. Natural selection that produces such traits is focused on individual organisms rather than species. Thus, the consequences of the traits for rates of speciation are incidental. Furthermore, the fixation of such a trait might have triggered an evolutionary radiation from the initial species that possessed it, but then ultimately have contributed to the extinction of a higher taxon after external conditions changed.

Not only do characteristic rates of speciation during adaptive radiation tend to vary greatly among taxa, but they correlate strongly with rates of extinction (Fig. 2.3.2.3). This correlation exists because, quite serendipitously, the same intrinsic factors tend to govern rates of speciation and rates of extinction (Stanley 1979, 1990). A high rate of speciation is advantageous in providing a high net rate of morphological change (especially if evolution is punctuational). At the same time, however, a high rate of evolutionary turnover creates numerical instability and a high risk of extinction. This is because a given fractional decline in rate of speciation or a given fractional increase in rate of extinction automatically produces a more rapid decline in number of species for a taxon with a high rate than for one with a low rate of turnover (Stanley 1979).

Behavioural complexity

Complex stereotypic behaviour tends to promote speciation by producing barriers to interbreeding between populations: a sophisticated reproductive ritual is easily disrupted. By rendering a taxon ecologically fragile, complex stereotypic behaviour also tends to elevate rate of extinction. This appears to be at least a partial explanation for the relatively high rates of evolutionary turnover in groups like ammonoids and mammals.

Niche breadth

Species with narrow niches are characterized by high probabilities of speciation, in part because such species tend to have unstable, patchy populations and in part because there are many potential new niches for their populations to invade through evolutionary divergence. Of course, because of their ecological specialization, such species are also vulnerable to extinction as a result of relatively minor environmental changes.

Population size and stability

Species with small and patchy populations tend to speciate relatively frequently because they produce spatial isolates readily. Of course, the small size and instability of such populations also elevate the probability of extinction. Modern pectinaceans (scallops) appear to illustrate these relationships. They are unusual among present-day epifaunal bivalves in commonly inhabiting exposed, as opposed to cryptic, settings; although they survive against predation by virtue of their ability to swim, heavy predation commonly results in relatively small, patchy populations. Their rates of extinction and speciation during the Neogene have been significantly higher than those of nearly all other bivalve taxa.

Dispersal ability

Dispersal ability is correlated with high rates of speciation in some taxa (Hansen 1980), but not in others. Differences among taxa appear to relate to the patchiness and stability of populations (Stanley 1990). For taxa with stable, relatively continuous geographical distributions, effective dispersal retards rate of speciation. In contrast, for taxa characterized by unstable, patchy populations, effective dispersal promotes speciation, e.g. the origin of larval brooding in ovicells appears to have triggered the Cretaceous adaptive radiation of cheilostome bryozoans (Taylor 1988).

Morphogenetic plasticity

Morphogenetic constraints appear to reduce the potential of certain taxa to generate new species. In other words, natural selection may not easily mould new adaptations from complex morphology that is the product of an intricate pattern of development. Taxa constrained in this way are often described as specialized forms. Unfortunately, specialization is difficult to define or quantify; to include a failure to diversify in any definition would entail circular reasoning. The tendency of cichlid fishes to undergo rapid evolutionary radiations has been taken to exemplify the importance of morphogenetic plasticity to diversification; the pharyngeal jaw apparatus of cichlids appears to evolve readily in a variety of adaptive directions (Liem 1973).

Ecological opportunities

External conditions, in addition to the inherent properties of taxa, influence rates of speciation. External conditions are ecological in nature and include both biotic and abiotic factors. Competition and predation are the two most important biotic factors. None the less, the decline of one taxon during the expansion of another similar taxon does not necessarily imply that competition with the second taxon promoted extinction or suppressed speciation in the first: simultaneous occurrence does not establish causal connection. Thus, the idea that the decline of the perissodactyls during the Neogene resulted from the expansion of the artiodactyls has not been borne out by detailed analysis, which shows that the two groups frequently expanded or contracted simultaneously. On the other hand, patterns of diversification and extinction indicate that the rodents may have defeated the multituberculates in competition during Palaeogene time.

Within-taxon competition may slow the rate of speciation as evolutionary radiation progresses, producing a sigmoid pattern of numerical increase (Fig. 2.3.2.1). None the less, during an interval of general biotic radiation, such as the initial Palaeozoic expansion of marine life, the impact of either competition from or predation by other radiating taxa may have played at least as large a role in slowing speciation as within-taxon competition.

New habitats

The appearance of a new habitat promotes rapid speciation of taxa that have access to it, by providing resources in the near-absence of competition and predation. Relatively youthful islands often preserve the products of evolutionary radiations, as do lakes, which amount to islands in a sea of land. One well-known example of insular radiation is that of *Drosophila* in the Hawaiian Islands, which yielded about 238 species in 5.6 million years. Another is the radiation of cichlid fishes in Lake Victoria, which produced about 170 species during only about 12 000 years (Johnson *et al*. 1996) (see Section 2.1.3). The fossil record documents a rapid radiation of gastropods when water level rose in the Pannonian Basin of eastern Europe about 10 million years ago (Geary 1990).

Aftermaths of mass extinction

Radiations that followed mass extinctions are equivalent to those triggered by the appearance of new habitats; they resulted from the availability of newly vacated habitats. Such radiations may have resulted from weakened competition in an impoverished ecosystem, but they may also have resulted from weak predation. Unfortunately, it is difficult to establish the relative importance of these two ecological factors. The most famous example of a postextinction radiation is that of the mammals following the dinosaurs' demise. Presumably, the dinosaurs, which benefited from a slight evolutionary head start in the Triassic, suppressed early mammals through both competition and predation. The importance of predation, though seldom discussed, is implicit in the customary portrayal of Cretaceous mammals as refugial creatures: ones that were not only small but in many cases arboreal, fossorial, or nocturnal.

Biotic provisioning

The evolutionary radiation of one taxon can stimulate the radiation of a second taxon for which the first represents a resource. For the adaptive radiations of flowering plants and insects since mid-Cretaceous time, the effect has apparently been mutual. Rates of speciation have been elevated in both groups by the ready isolation of daughter populations from parent species by minor changes in insect behaviour and flower morphology. In addition, because of this linkage between their modes of reproductive isolation, insects and flowering plants appear to have radiated synergistically: the reproductive linkage has accelerated rates of speciation in both groups.

The role of adaptive breakthroughs

Many evolutionary radiations have been triggered by the origin of adaptive innovations (see Section 2.3.1). Although such an innovation is an intrinsic feature of a taxon, its role is similar to that of the three avenues to new ecospace: the appearance of a new habitat, the extinction of pre-existing taxa, and the provisioning of new ecospace by another radiating taxon. These factors are not mutually exclusive: a radiation that follows a

major extinction or the provision of a new habitat is usually amplified by the evolution of adaptive breakthroughs. An adaptive breakthrough can crop up in any taxon, increasing its potential to radiate. The initial fixation of such a breakthrough within a population usually results from the same adaptive value that subsequently promotes speciation. The polyphyletic origin of tall teeth in horses described earlier exemplifies this relationship. Taller teeth evolved anagenetically within some well-established species and also tended to evolve within populations during speciation events, but then the presence of tall teeth elevated rates of speciation within those species that possessed them.

One form of evidence that a particular adaptive trait triggered an evolutionary radiation is the observation that closely related taxa that lacked the trait failed to diversifiy rapidly. The case is strengthened if such a trait was present in more than one taxon that radiated or was absent in more than one taxon that failed to do so. None the less, any argument that a particular trait triggered rapid radiation must be grounded in functional morphological analysis indicating that the trait in question should have opened new ecological opportunities.

References

Cheetham, A.H. (1986) Tempo of evolution in a Neogene bryozoan: rates of morphologic change within and across species boundaries. *Paleobiology* **12**, 190–202.

Eldredge, N. and Gould, S.J. (1972) Punctuated equilibria: an alternative to phyletic gradualism. In: T.J.M. Schopf, ed. *Models in paleobiology*, pp. 82–115. Freeman and Cooper, San Francisco.

Geary, D.H. (1990) Patterns of evolutionary tempo and mode in the radiation of *Melanopsis* (Gastropoda; Melanopsidae). *Paleobiology* **16**, 492–521.

Hansen, T.A. (1980) Influence of larval dispersal and geographic distribution on species longevity in neogastropods. *Paleobiology* **6**, 193–207.

Hulbert, R.C. (1993) Taxonomic evolution in North American Neogene horses (subfamily Equinae): the rise and fall of an adaptive radiation. *Paleobiology* **19**, 216–234.

Johnson, T.C., Scholz, C.A., Talbot, M.R. *et al.* (1996) Late Pleistocene desiccation of Lake Victoria and rapid evolution of cichlid fishes. *Science* **273**, 1091–1093.

Liem, K.F. (1973) Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. *Systematic Zoology* **22**, 425–441.

Stanley, S.M. (1979) *Macroevolution: pattern and process*. W.H. Freeman, New York. (Paperback edition with new introduction, 1998. Johns Hopkins University Press, Baltimore.)

Stanley, S.M. (1990) The general correlation between rate of speciation and rate of evolution: fortuitous causal linkages. In: R.M. Ross and W.D. Allmon, eds. *Causes of evolution: a paleontologic perspective*, pp. 103–127. University of Chicago Press, Chicago.

Stanley, S.M. and Yang, X. (1987) Approximate evolutionary stasis for bivalve morphology over millions of years. *Paleobiology* **13**, 113–139.

Taylor, P.D. (1988) Major radiation of cheilostome bryozoans: triggered by the evolution of a new larval type? *Historical Biology* **1**, 45–64.

2.3.3 Competition in Evolution

J.J. SEPKOSKI Jr

Introduction

Ecological competition refers to the ability of a local population of one species to reduce the rate of expansion or the local population size of another species. This is accomplished by interference rather than by predation or parasitism. Interference can involve consumption of common resources, such as food or habitat space; disturbance, such as altering substrate conditions; or indirect effects, such as attracting common predators or parasitoids (see review by Sepkoski 1996).

Competition and macroevolution

Competition has been invoked throughout the history of evolutionary biology as a reason why some clades of organisms are 'successful' while others are 'unsuccessful'. Darwin (1859) used the principle of competition, derived from Adam Smith's economics, to address his critics. Natural selection would only adapt species to their immediate environments, but many of Darwin's contemporaries saw progressive change in the history of life. Darwin's solution was that interactions among species vying for common resources must favour those most capable of capturing resources. His famous metaphor was a myriad of wedges of different sizes and shapes being driven into a surface; some would be driven deeper and would squeeze out other wedges (see Gould and Calloway 1980).

Darwin's explanation why some taxa become extinct while others proliferate has been a common explanation for biotic change since his time. Yet, in modern ecology, a quantitative and predictive understanding of competition has involved analysis of interactions between populations at the local level on generational time scales: organisms that would see one another, degrade the local environment for others, or locally attract enemies for others. Many empirical studies have indicated that competitive exclusion (i.e. local extinction of one species) usually occurs over scales of tens of generations. How this translates into competitive extinction of species at

time scales preserved in the fossil record is not immediately clear. Thus, any statement that 'species of clade 1 outcompeted species of clade 2' is suspect.

Arguments against competition in macroevolution

Numerous analyses have attempted to refute the idea that ecological competition is a factor in macroevolution. Well-known examples of putative competitive displacement, such as brachiopods by bivalves and synapsids ('mammal-like reptiles') by dinosaurs, have been roundly criticized. Brachiopods were dominant members of the Palaeozoic evolutionary fauna but are relatively depauperate today. Bivalves have a reverse history and are abundant members of the Modern marine fauna. Because both are two-shelled animals, mainly sessile suspension-feeders, and abundant in shelf environments, many workers have asserted that the waning of brachiopods and waxing of bivalves through the Phanerozoic was the result of competitive displacement. However, Gould and Calloway (1980) argued, to the contrary, that the waning and waxing were independent histories, influenced uniquely by the end-Permian mass extinction. Each group's diversification (Fig. 2.3.3.1) was positively correlated before and after the end-Permian, but their *total* rates of diversification were reset by that massive event such that the rate of diversification of bivalves increased whereas the rate of brachiopods decreased. Thus, these two groups were but 'ships that pass in the night'.

A similar case has been argued for the success of dinosaurs over synapsids near the end of the Triassic (Benton 1983). Data, again on taxonomic diversity, point to the replacement of synapsids being in no sense 'progressive' but rather a result of extinction events during which dinosaurs survived preferentially, just as bivalves had done at the end-Permian. More extensive analyses of diversity data for all tetrapod families have suggested that at most only 13% of replacements seen in the fossil record could possibly be ascribed to competitive displacement (Benton 1996 and references therein).

Arguments for competition in macroevolution

Direct observation of competition in the fossil record

All of the arguments summarized above, from Darwin to the present, used observations of waxing and waning of taxonomic importance. Therefore, the arguments for or against competition as a force in macroevolutionary change are indirect. But ecological competition can be observed directly in the fossil record, albeit in very special situations. An example is encrusting colonies of bryozoans in the orders Cyclostomata and Cheilostomata that grow on hard substrates (McKinney 1995). As colonies grow and encounter one another, there is direct competition for habitat space. The winner overgrows the loser, and this is recorded in fossil specimens. Analyses of successful overgrowths through the Cretaceous and Tertiary tabulate that cheilostome bryozoans overgrew cyclostomes in 66% of preserved encounters. Yet, despite their local competitive disadvantage, cyclostomes seem to have suffered little evolutionary decline (Lidgard *et al.*

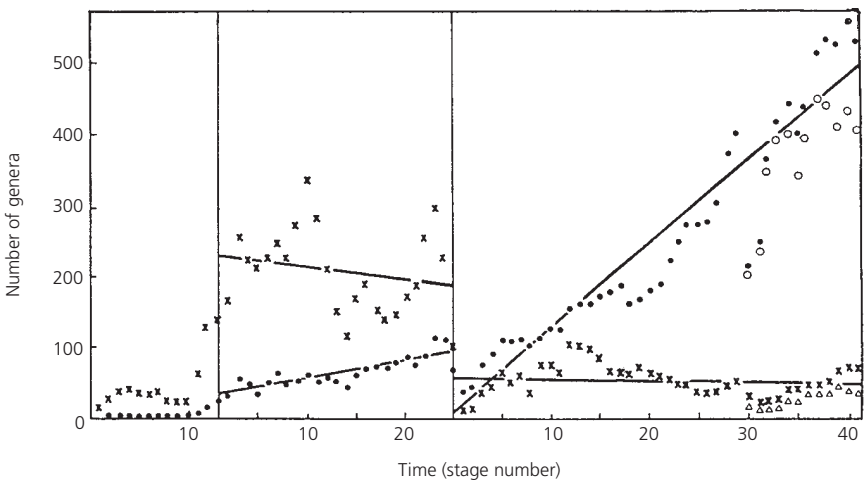

Fig. 2.3.3.1 Genus diversities of brachiopods (×) and marine bivalves (•) through the Phanerozoic (see Gould and Calloway 1980). Diversities can be recalculated to remove some of the effects of the pull of the Recent for brachiopods (▵) and marine bivalves (○). Time is stage number from the standard stratigraphic subdivision of the Phanerozoic, numbered from the beginning of the Cambrian (left-hand of the graph), from the Middle Ordovician (first vertical line), and from the beginning of the Triassic (second vertical line). Regression lines through the points are least-square fits to linear trends in the global diversities of brachiopods and bivalves before and after the end-Permian mass extinction. (Modified from Sepkoski 1996.)

1993), although this conclusion is open to reinterpretation. (The same models used below have been applied to the cheilostome/cyclostome system, suggesting that there was indeed a macroevolutionary effect; Sepkoski *et al*. 2000.)

Modern arguments for competition in macroevolution

Various workers in recent years have considered both ecological theory concerning population-level competition and macroevolutionary critiques to develop specific models of displacement in the fossil record. An interesting example is the case of the replacement of North American multituberculate mammals by rodents during the early Tertiary. It has been argued that these two groups of species could be concurrent in the fossil record only because they were initially geographically isolated (Krause 1986). Invasion of rodents into the range of multituberculates led to the latter's extinction in North America. However, this hypothesis does not explain a geologically short but perceptible co-occurrence of multituberculates and rodents, given the rapidity of observed competitive displacements in modern communities.

An answer to many of these problems may be the ecological principle of incumbency (Rosenzweig and McCord 1991). An incumbent is an established species with large local population numbers that can exclude invaders into the local environment by sheer inertia, even if the invaders are competitively superior. However, if something external to the incumbent's favour decimates its population (e.g. poor larval recruitment, typhoons) the other species may colonize and exclude the former incumbent. This is a process that may take place in local populations over geologically perceptible amounts of time and therefore preserve both loser and successor concurrently in the fossil record.

Other scenarios of ecological competition leading to clade displacement are also plausible (see Sepkoski 1996). All scenarios involve processes in addition to local ecological competition among populations, such as evolutionary adaptation or environmental change. Examples include: one species evolving to usurp more and more of its competitors' resources (or attracting more of its competitors' enemies); environmental change reducing one competitor's superior habitats or refuges; and gradual invasion of one competitor's related taxa, increasing diffuse competition. The importance of these scenarios is that they make it plausible to observe gradual decline of a competitive inferior at time scales resolvable in the fossil record. The problem with these scenarios is how to test them with fossil data.

Models of displacement resulting from competition

Considered in terms of clade replacement, the problem becomes how to test patterns of taxonomic diversity through time with respect to predictions of displacement resulting from local ecological competition. The traditional criterion has been that one clade wanes while the other waxes—the so-called 'double wedge' pattern. This leaves little room for testing more subtle patterns of long-scale diversification, especially given the frequent extinction events of the Phanerozoic. If it is assumed that clades diversify multiplicatively and their diversities are limited by some common resources, disturbances, or enemies, then their global diversifications over time can be described, to a first approximation, by coupled logistic equations:

$$\mathrm{d}D_i/\mathrm{d}t = \frac{r_i D_i\left(D_i - \Sigma D_j/\hat{D}_i\right)}{j}$$

where D_i is the species diversity of interest; t is time; r_i is the rate of diversification of clade i at minimal diversity; $\hat{D}_i$ is its effective maximum, or equilibrium, diversity; and D_j is the species numbers of all clades j with which species of clade i interact competitively (see also Miller and Sepkoski 1988; Sepkoski 1996).

This model of interaction among species in various clades is closely related to the classic Lokta–Volterra equations that have been used by ecologists to describe local population sizes of competing species in local environments. The relationship exists because there is a topological equivalence between population genealogies and species phylogenies in their branching geometries. The coupled-logistic equation has interesting mathematical and predictive features. Mathematically, it cannot be formally integrated because it is a coupled quadratic differential; each clade j is modelled with the same equation. Therefore, solutions must be computed numerically. This permits, on the other hand, changes in parameters during numerical solution. For example, an extinction event can be modelled as a lowering of $\hat{D}_i$ (which would happen if extinction rates were increased abruptly or gradually by some external forcing factor; see Sepkoski 1996).

The predictive power of the model of clade displacement comes from the kinds of qualitative and quantitative patterns that can be computed for groups of clades with different rates of diversification, characteristic diversities, and histories with respect to extinction events. Two immediate predictions follow:

1 Clades with locally competing species should exhibit non-linear patterns of diversity through time, quite different from a double wedge (in a two-clade situation). In fact, the clade with mostly competitively inferior

species is predicted to exhibit exponential decay of diversity through time, whereas the clade with 'superior' species should exhibit either exponential increase or sigmoidal increase, if its diversity is approaching its limit ($\hat{D}_i$).

2 Rates of recoveries from mass extinctions of surviving clades can be very instructive about possible interaction. The model predicts that clades can diversify in unison if their diversities are below the limit for each ($\hat{D}_i$). Such a situation can occur during recoveries from extinction events as well as during initial radiations. The coupled model predicts that it is the observed *rates* at which diversification occurs that are important. If at a mass extinction clade 1 disappears, the prediction is that surviving clade 2, whose species formerly competed with those of 1, will exhibit a faster rate of diversification than during clade 2's initial radiation when clade 1 was extant. If both clade 1 and clade 2 survive, then the prediction is that the clade with mostly competitively inferior species will exhibit progressively slower rates of recovery after each extinction event as the other clade retains more and more diversity (for detail, see Sepkoski 1996).

An example of these predictions is illustrated by the model solution in Fig. 2.3.3.2. Two clades with competing species originate at the same time. Clade 1 has a higher rate of diversification but packs fewer species into the environment, which is formalized as a lower $\hat{D}_1$. Clade 2 has a lower rate of diversification but packs in more species, usurping the ecospace of clade 1's species. Approximately midway through their histories there is a mass extinction.

Early in the model history, the diversities of the two clades are positively correlated. Well before the mass extinction, clade 1 approaches its limit of diversity, $\hat{D}_1$, and actually declines somewhat as clade 2 continues slow diversification. At the mass extinction, both clades lose diversity and then recover in the aftermath. However, clade 1 diversifies more slowly than during its initial radiation because clade 2 now has substantially more diversity. This difference in rate for clade 1 could be analytically assessed by plotting the logarithm of its diversity against linear time for the initial radiation and for the postextinction recovery; the slope of the locus of points would be the realized per-taxon rate of diversification. In Fig. 2.3.3.2, the difference in rate of diversification after the mass extinction is shown by dotted lines that represent the diversity of clade 1 if all species of clade 2 had disappeared. The shaded spindle instead illustrates the non-linear trajectory of clade 1 to extinction as the competitively superior species of clade 2 usurp the common environment and diversify.

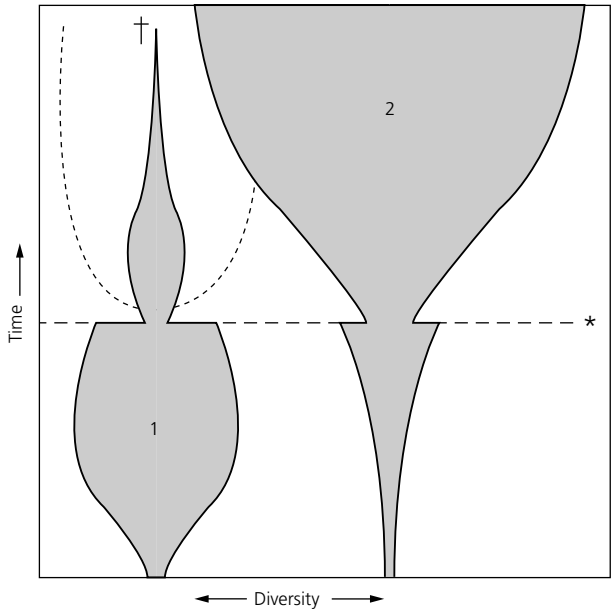

Fig. 2.3.3.2 A model solution for the histories of diversity of two clades with competing species. Their relative diversities are illustrated as spindle diagrams, symmetrical about each vertical axis. The dashed horizontal line marked by an asterisk is a modelled mass extinction. The cross marks the extinction of clade 1 whereas the dotted lines about clade 1 indicate its history of diversity had clade 2 been extinguished at the mass extinction. See text for further explanation. (From Sepkoski 1996.)

A classic case study from the fossil record: 'Ships that pass in the night'?

Gould and Calloway (1980) argued that possible competitive interaction among species of articulate brachiopods and marine bivalves could not have influenced the histories of diversity of the two clades (Fig. 2.3.3.1). This conclusion was based on linear fits to data and on positive correlation of patterns of diversity before and after the end-Permian mass extinction. However, the model for patterns of clade displacement predicts non-linear patterns as well as intervals of positive correlation through time.

Major trends in the diversity of brachiopods and bivalves, as well as extinction events and recoveries of diversity, are illustrated in Fig. 2.3.3.3(a), which is an interpretation of the data in Fig. 2.3.3.1. As opposed to the linear regressions in Fig. 2.3.3.1, Fig. 2.3.3.3(a) emphasizes non-linear patterns. Figure 2.3.3.3(b) is a model solution, parameterized by measured rates of diversification, apparent maximum diversities, and the magnitude of the end-Permian event for fossil genera of brachiopods and bivalves. The interpreted empirical pattern and the model solution are similar, leaving open

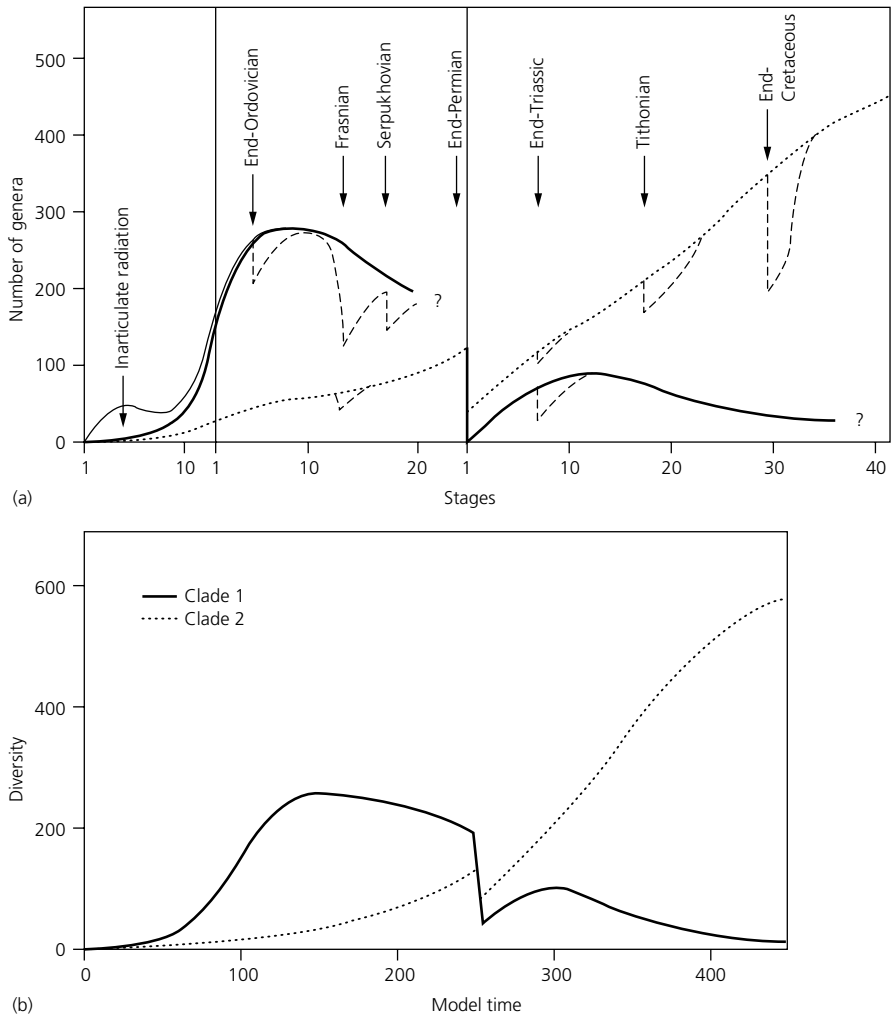

Fig. 2.3.3.3 Interpretation and model of the histories of brachiopod and marine bivalve diversity. (a) Interpretation of Fig. 2.3.3.1 with major trends of brachiopods illustrated by the solid line and of bivalves by the dotted line. Dashed lines indicate extinction events and recoveries, as labelled. (b) Solution of the coupled logistic model for two clades scaled to evolutionary rates of brachiopods (solid line) and bivalves (dotted line) with a perturbation (simulated mass extinction) near the position of the end-Permian event. The model solution is shorter after this event than the interpreted data because simple numbering inflates the magnitudes of Mesozoic and Cenozoic stages, which are short relative to Palaeozoic units. (Modified from Sepkoski 1996.)

the hypothesis that the histories of diversity of the species of these two clades may indeed have been influenced by evolutionary response to competition among their species in local shelf environments.

Conclusions

One case study does not demonstrate Darwin's invocation of ecological competition as a major process of biotic change over time. Furthermore, analyses of patterns of global taxonomic diversity through geological time constitute only circumstantial evidence. It would be preferable to have compatible results from multiple experiments; these could include consistent changes in observed rates of diversification after a series of mass extinctions, as predicted by the coupled logistic model, or consistent replacement in isolated geographical (or environmental) areas (as Rosenzweig and McCord 1991 demonstrated for displacement of straight-necked by flexible-necked turtles during the Tertiary). Other criteria include: (1) overlap in environmental and geographical distribution, which could be minimal if ecological competition among species were intense; (2) ecofunctional evidence of consumption of common resources; (3) disturbance of habitat by species of one or both clades; and (4) attraction of common enemies.

Not all of these lines of evidence for competition in macroevolution are easily demonstrated in the fossil record, although evidence from diversity, morphology, geographical distribution, and environmental change have been employed to argue that aphorrhaid gastropods were displaced by stromboid gastropods through the Tertiary (Roy 1996). Yet even with this level of evidence and with predicted non-linear histories of diversity, it is difficult to distinguish between competi-

tion among species at the clade level vs. interaction of species within larger units, such as evolutionary faunas, with different ecological structures (see Miller and Sepkoski 1988; Sepkoski 1996). Further analyses and expanded theory are needed to clarify to what extent populations competing in local environments have shaped macroevolutionary history.

References

Benton, M.J. (1983) Dinosaur success in the Triassic: a non-competitive ecological model. *Quarterly Review of Biology* **58**, 29–55.

Benton, M.J. (1996) On the non-prevalence of competitive replacement in the evolution of tetrapods. In: D. Jablonski, D.H. Erwin and J.H. Lipps, eds. *Evolutionary paleobiology*, pp. 185–210. University of Chicago Press, Chicago.

Darwin, C. (1859) *On the origin of species by means of natural selection*. John Murray, London.

Gould, S.J. and Calloway, C.B. (1980) Clams and brachiopods—ships that pass in the night. *Paleobiology* **6**, 383–396.

Krause, D.W. (1986) Competitive exclusion and taxonomic displacement in the fossil record: the case of rodents and multituberculates. In: K.M. Flanagan and J.A. Lillegraven, eds. *Vertebrates, phylogeny and philosophy*, pp. 95–117. University of Wyoming, Laramie, Wyoming.

Lidgard, S., McKinney, F.K. and Taylor, P.D. (1993) Competition, clade replacement, and a history of cyclostome and cheilostome bryozoan diversity. *Paleobiology* **19**, 352–371.

McKinney, F.K. (1995) One hundred million years of competitive interactions between bryozoan clades: asymmetrical but not escalating. *Biological Journal of the Linnaean Society* **56**, 465–481.

Miller, A.I. and Sepkoski, J.J. Jr (1988) Modeling bivalve diversification: the effect of interaction on a macroevolutionary system. *Paleobiology* **14**, 364–369.

Rosenzweig, M.L. and McCord, R.D. (1991) Incumbent replacement: evidences for long-term evolutionary progress. *Paleobiology* **17**, 202–213.

Roy, K. (1996) The roles of mass extinction and biotic interaction in large-scale replacements: a reexamination using the fossil record of stromboidean gastropods. *Paleobiology* **22**, 436–452.

Sepkoski, J.J. Jr (1996) Competition in macroevolution: the double wedge revisited. In: D. Jablonski, D.H. Erwin and J.H. Lipps, eds. *Evolutionary paleobiology*, pp. 221–255. University of Chicago Press, Chicago.

Sepkoski, J.J. Jr, McKinney, F.K. and Lidgard, S. (2000) Competitive displacement between post-Paleozoic cyclostome and cheilostome bryozoans. *Paleobiology* **26**, 7–18.

2.3.4 Biotic Interchange

D.R. LINDBERG

Introduction

Biotic interchange is one of the most temporally and spatially fluid of all phenomena in organismal biology. The term can be used to describe the almost instantaneous transfer of a plant virus from a natural forest to an adjacent agricultural field, or the wholesale movement of a fauna or flora between continents over millions of years. With such broad usage and scalability, it is not surprising that the mechanisms and implications of biotic interchange are often controversial.

A comparative and systematic approach to the investigation of biotic interchange today, applicable at multiple temporal and spatial scales, needs to consider the following questions (Vermeij 1996).

1 How do invaders differ from non-invaders in the arrival, establishment, and integration phases of invasion?

2 How do donor regions or communities that have produced many successful invaders differ from those in which few resident species have been able to extend their ranges?

3 How do recipient ecosystems with many successfully established invaders differ from those in which few species have taken hold?

4 How does invasion affect the evolution not only of the invader itself but also of species in the recipient community with which the invader interacts?

Variables and scales of biotic interchange

Biotic interchange begins with the arrival of an individual in a region outside the taxon's existing distribution. In Recent habitats with high probabilities of human-mediated introductions (e.g. as a result of international commerce), introductions may exceed one new species every 12 weeks. However, most appear to be unsuccessful due to low densities, physiological or life history limitations, lack of suitable habitat, predation, or competition with indigenous taxa. Unsuccessful biotic interchange is unlikely to be evident in the fossil record; patterns that are discernible undoubtedly result from successful events that accumulate over geological time (Fig. 2.3.4.1). Rates of introductions in the past are, not unexpectedly, significantly lower than those occurring due to human agency today. Successful Pliocene and Pleistocene migrations of nearshore marine invertebrates between the temperate regions of North and South

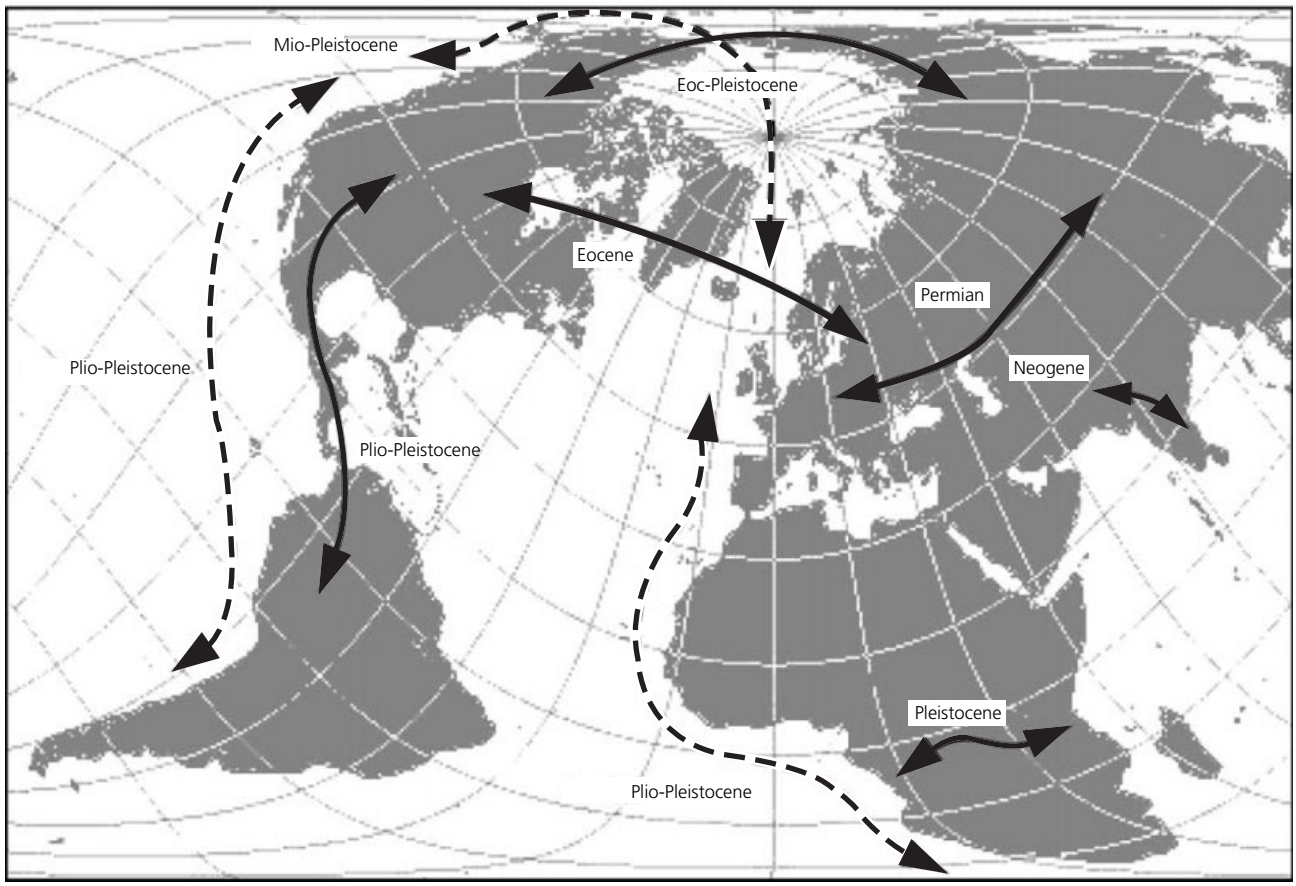

Fig. 2.3.4.1 Partial world map of the current configuration of continents showing the timing and extent of selected biotic interchange events discussed in the text. Dashed lines indicate nearshore marine events; solid lines indicate terrestrial events. Note the variability of spatial and temporal scales of events.

America averaged about 2.7 taxa/myr for the Pliocene and 2.8 taxa/myr for the Pleistocene (Lindberg 1991).

Palaeontological studies of biotic interchange document changing distributions of animals and plants through time, and correlate these changes with physical and biotic events and perturbations. These patterns may involve species or genera (e.g. the introduction of *Astarte* spp. into the North Pacific) or substantially higher taxonomic categories (e.g. the stampede of Amniota between the Americas). Incomplete biostratigraphy can obviously complicate interpretation, but a much greater danger is the use of taxonomy as a surrogate for phylogeny for recognition and comparison of disjunct biotic patterns. Whether a taxon has rafted into a new region via crustal plate segments or the water column, the 'smoking gun' of such an event is the recognition of a relationship between the disjunct taxa. However, most taxa lack a modern phylogenetic treatment and sister-taxon status has not been established for many of the classical examples cited in the literature. Most workers use ranks within the Linnaean classification as a proxy for relatedness in the absence of phylogenetic hypotheses. Given the danger of confusing common ancestry with convergence, all putative patterns require independent assessment and demonstration of the phyletic relationships among the organisms before biotic interchange is invoked.

Patterns of biotic interchange can be elucidated with area cladograms, which reflect relationships between areas or regions. Where taxon relationships are congruent with the area cladogram, a vicariance model of their biogeographical history can be falsified in favour of a more traditional dispersal model. However, dispersal and vicariance need not be cast as diametrically opposed processes. The closing of the Panamic portal, for example, produced a vicariance event that separated Caribbean and tropical eastern Pacific marine organisms. At the same time, the perturbations to tropical current patterns caused by the emerging isthmus appear to have facilitated the interchange of temperate marine organisms between the north-eastern and south-eastern Pacific (Lindberg 1991), initiated a new round of Pacific

and Atlantic interchanges (Vermeij 1992), and started the Great American Biotic Interchange (Stehli and Webb 1985).

The dynamic and complex nature of interactions between organisms and a varying environment also makes recognizing biotic interchange in the fossil record problematic, especially when regional extinction has occurred. The bivalve mollusc *Mya arenaria*, for example, has a broad geographical range occurring on both coasts of the Atlantic Ocean and along the east coast of the Pacific Ocean. However, fossils indicate that *M. arenaria* first appeared in the Miocene of the Pacific and invaded the Atlantic during the Pliocene. Regional extinction of *M. arenaria* along the east coasts of the Pacific and Atlantic oceans during the Pleistocene left the taxon present only in the western Atlantic. From here, it was reintroduced by human activity into the eastern Pacific and Atlantic oceans and the Black Sea. An incomplete fossil record or lack of knowledge regarding human introductions could produce a very different interpretation of the history of *M. arenaria* in the Northern Hemisphere.

Biotic interchanges may not be single events. Fossil horses, which have been commonly used as a textbook example of evolution, provide an excellent example of multiple interchanges. MacFadden (1992) reconstructed biotic interchanges based on phylogenetic relationships and suggested that Equidae may have originated in Asia (based on sister-taxa affinities) and migrated from there to North America and northern Europe. The equids then underwent a vicariant event in the early Eocene, when the DeGeer land bridge between North America and Scandinavia broke apart leaving sister taxa in Europe and North America. This was then followed by four major dispersals of horses out of North America during the Late Eocene (hyracotheres), Early Miocene (anchitheres), Late Miocene (hipparions), and again in the Plio-Pleistocene (*Onohippidium*, *Hippidion*, and *Equus*).

Equid interchange to the south across the Isthmus of Panama was not a unique event either. Two taxa (*Onohippidium* and *Hippidion*) appear to have arrived in South America during the Pliocene. However, *Equus* did not arrive until ≈1.5 Ma. All three taxa appear to have coexisted until ≈10 Ka when horses, along with many other large mammals, became extinct in South America. Without a detailed knowledge of horse relationships, it is not possible to recognize the complexity and structure of the equid biotic interchanges.

Examples from the Great American Biotic Interchange

Horses were not the only component of the New World mixing of indigenous and immigrant mammals typically referred to as the 'Great American Biotic Interchange' (GABI), nor was all the movement from north to south. North American immigrants to South America included llamas, mastodons, tapirs, bears, and sabre-tooth cats, as well as horses. From the south came armadillos, opossums, and anteaters, as well as the phorusrhacid terror bird, the only large cursorial carnivore from South America to take part in the GABI. But the final outcome of the GABI was decidedly asymmetric. Webb (1991) concluded that the land mammal interchange was roughly equal on both continents, and the impact of the interchange was not detectable in North America after about 1 myr. North American mammals speciated at exponential rates in South America, however, while extinctions of immigrant taxa in North America were about three times higher at the familial rank than they were for immigrant taxa in South America. This combination of higher speciation rates and lower extinctions for immigrant mammals in the south generated the asymmetric pattern. Webb (1991) proposed a two-phase ecogeographical model involving changes in the habitat, i.e. the relative extent and size of rain forest and savannah development during glacial cycles.

A consideration of the relative importance of trophic niche, continent of origin, and body size in the extinction patterns of living South American mammals following GABI showed that only body mass is correlated significantly with the probability of extinction (Lessa and Farina 1996). Immigrants from North America were not more resistant to extinction and, contrary to conventional wisdom, marsupials did not go extinct more often than placentals following the interchange. Thus, the subsequent success of North American immigrants in South America was due solely to their higher speciation rate and not a lower extinction rate. Data for North American Late Pleistocene mammals corroborate the discovery that body mass was the only factor associated with the higher probabilities of extinction, both in the north and the combined dataset (Lessa *et al.* 1997). Thus, the common explanation that competitive displacement was responsible for the asymmetric pattern of biotic interchange between North and South America is not supported.

Body mass data for South American terrestrial mammals show the unmistakable effect of the GABI on the living South American fauna. At a continental scale the distribution of body masses for South American mammals is highly right skewed and possesses several modes (Marquet and Cofre 1999). A smaller-sized mode corresponds to species derived from North American immigrants, while a larger-sized mode represents indigenous South American lineages. Thus, it is possible to identify historical components of biotic interchange at different spatial scales, and to explore the ways biotas are built.

Patterns and processes of biotic interchange

While the GABI is undoubtedly one of the most studied, there are numerous other examples in terrestrial habitats with different patterns and causalities. The Neogene Siwalik formations of India and Pakistan preserve an excellent vertebrate record, with good chronostratigraphic control, which documents fluctuations in diversity (Barry *et al.* 1991). Detailed analyses (Barry *et al.* 1991) revealed that, in contrast to the GABI, increases in taxon diversity were primarily the result of immigration rate not speciation rate, extinction rates may have been greater for immigrant rather than indigenous taxa, and the overall changes in diversity appeared independent of relative abundance and body size. From this comparison it is evident that the outcomes of biotic interchanges may not be similar even if the same taxon (e.g. Mammalia) is involved. Local conditions appear to be more important than global ones, and advantages or vulnerabilities present in any immigrant or indigenous taxon are most likely emergent at lower taxonomic ranks and are dependent on the temporal and spatial context of the interchange. A large stochastic component is also likely to be present in most interchange events.

Animals are not the only organisms to participate in biotic interchanges. Plants have long been known to respond to changes in palaeoclimates. The Great Eurasian Floral Interchange occurred during the Late Permian when the flora of western Europe moved over the Russian platform into present-day Mongolia (Angara). Floral components also came from southern China through northern China. However, migration of the resident flora out of Angara into neighbouring regions was limited and the overall direction of the interchange was asymmetric. In addition to body fossils, pollen stratigraphy provides insights into floral movement and interchanges—sometimes at impressive levels of resolution. For example, pollen records from Africa document changes between warm–dry and cold–moist climates, and corresponding shifts in the extent and distribution of montane forests. During the cold and moist conditions of the last glacial maximum montane forests were found to be widespread in some regions and probably aided biotic interchange of floras between the highlands of East and West Africa.

While biotic interchanges involving plants are typically interpreted as floras responding to climate change, there is little doubt that the associated faunas moved in unison. In contrast to the plants, animal biotic interchanges are more often attributed to large-scale vicariance events—particularly terrestrial taxa and faunas—or the dispersal of individual taxa in marine systems. But here too, there is little doubt that associated floras moved in unison with faunas during vicariant events, or were dispersed with other propagules in the water column irrespective of chlorophyll content.

After interchange

While the underlying mechanisms that make biotic interchange possible can often be determined from the stratigraphic record, the subsequent processes that produce the signature of a biotic interchange are more difficult to deduce. Abundance has been identified as the most likely variable in determining the initial success or failure of recent biotic invasions (Williamson and Fitter 1996). For plants, abundance or propagule pressure can be even more important than life history and reproductive behaviour, and this is likely true for animals as well. Propagule pressure today is closely associated with human activities and the constant transport and mixing of biomes and regions—the more opportunities the higher the probability of a successful introduction. While studies of biotic interchange in the fossil record cannot resolve the details of the initial invasion(s), the principle of uniformitarianism implies that abundance was also the key to successful events in the past. In the absence of human activities, the number of opportunities per unit time were undoubtedly several orders of magnitude less, but the vastness of geological time provided many opportunities for the most abundant taxa.

Documentation of the outcomes of interactions between indigenous taxa and coinvaders typically evoke classic ecological interpretations, such as competition or predation. However, there is little empirical evidence to support such interpretations (Vermeij 1991). Instead many of the outcomes appear to be based on stochastic events interacting with individual taxa or clades. Thus, subsequent ecological interactions may play less of a role in regulating biotic interchanges than previously thought, both in the Recent and the past. One possible indication of the decoupling of biotic interactions from the success or failure of an invader is the role of immigrants in trophic interactions in the new regions. For example, the temperate nearshore rocky communities of the Northern and Southern hemispheres of the New World appear to be mosaics of cosmopolitan species, indigenous species, and species that immigrated between Northern and Southern hemispheres. Although some communities appear to be products of interchange (e.g. kelp forests of California and Chile), only the taxa have immigrated; linkages and interactions between species are independent and often locally derived (Lindberg 1991). Thus, in studies of fossil communities, the inferred ecological role of a taxon in the source area may not be transferable or deducible in its new setting.

Testing among alternative processes

The questions listed in the introduction focus on the subsequent processes that produce the signature of a biotic interchange, and they provide starting points for further parsing the disparate scales of Recent and fossil interchange events. Vermeij (1996) asked 'How do invaders differ from non-invaders in the arrival, establishment, and integration phases of invasion?' One important character identified for Recent invasions is taxon abundance. Does a similar relationship exist for fossil taxa? Explicit comparisons are needed between palaeosettings of donor regions or communities that have produced successful invaders and those that have not; data could be gleaned from many of the well-documented case studies. A similar approach could be used to examine how palaeocommunities with numerous invaders differ from those in which few take hold. Such palaeobiological studies are of special importance because their temporal framework allows communities that resist to be compared with those that acquire invading taxa. Lastly, palaeobiological studies provide the only opportunity to examine how invasion affects the evolution of the invader as well as the species with which it interacts.

References

Barry, J.C., Morgan, M.E., Winkler, A.J., Flynn, L.J., Lindsay, E.H., Jacobs, L.L. and Pilbeam, D. (1991) Faunal interchange and Miocene terrestrial vertebrates of southern Asia. *Paleobiology* **17**, 231–245.

Lessa, E.P. and Farina, R.A. (1996) Reassessment of extinction patterns among the Late Pleistocene mammals of South America. *Palaeontology* **39**, 651–662.

Lessa, E.P., Van Valkenburg, B. and Farina, R.A. (1997) Testing hypotheses of differential mammalian extinctions subsequent to the Great American Biotic Interchange. *Palaeogeography, Palaeoclimatology, Palaeoecology* **135**, 157–162.

Lindberg, D.R. (1991) Marine biotic interchange between the northern and southern hemispheres. *Paleobiology* **17**, 308–324.

MacFadden, B.J. (1992) *Fossil horses: systematics, paleobiology, and evolution of the family Equidae*. Cambridge University Press, Cambridge.

Marquet, P.A. and Cofre, H. (1999) Large temporal and spatial scales in the structure of mammalian assemblages in South America: a macroecological approach. *Oikos* **85**, 299–309.

Stehli, F.G. and Webb, S.D. (1985) *The Great American Biotic Interchange*. Plenum Press, New York.

Vermeij, G.J. (1991) When biotas meet: understanding biotic interchange. *Science* **253**, 1099–1104.

Vermeij, G.J. (1992) Trans-equatorial connections between biotas in the temperate eastern Atlantic. *Marine Biology* **112**, 343–348.

Vermeij, G.J. (1996) An agenda for invasion biology. *Biological Conservation* **78**, 3–9.

Webb, S.D. (1991) Ecogeography and the Great American Interchange. *Paleobiology* **17**, 266–280.

Williamson, M.H. and Fitter, A. (1996) The characters of successful invaders. *Biological Conservation* **78**, 163–170.

2.3.5 Importance of Heterochrony

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Introduction

Heterochrony can be defined as change to the timing and rate of development. Each individual organism has an ontogeny—its life history, from the moment of conception until death. As organisms develop, from an initial egg or spore, through larva or embryo to juvenile and then adult, they not only increase in size but also undergo changes in shape. Furthermore, most organisms have a finite period of growth, often terminated by the onset of sexual maturity, when growth slows down appreciably or stops. Different individuals grow at different rates, and for different durations, as do different species. Furthermore, different parts of a single individual may grow for different lengths of time and at different relative rates. Heterochrony is change to the rate and duration of growth of all or part of an organism, compared with its ancestor.

Heterochrony can be regarded as the third part of the evolutionary triangle. At one corner is natural selection, at the second corner is genetics, and at the third is heterochrony. Take out any one corner and the triangle disappears and evolution does not occur. Genes control the growth of an organism and determine, in part, its morphological, physiological, and behavioural characteristics. Certain genes, in particular *Hox* genes, control the timing of expression of growth factors that determine when and where a morphological structure develops during ontogeny and for how long. Variations between individuals in the duration and rate of growth of all or part of the organism result in morphological differences. In populations of a species this is called intraspecific variation. These variants, induced by heterochronic changes, are then subjected to natural selection. Given this key role in providing much of the raw material upon which natural selection works, heterochrony consequently is a very important factor in evolution (McKinney and McNamara 1991; McNamara 1997).

Defining heterochrony

Heterochrony can take many forms. Compared with an ancestor, a descendant (either a descendant species or individual within a population) can show 'less' growth of particular morphological features or 'more' growth. If there is less growth during ontogeny, the descendant adult will resemble the juvenile condition of the ancestor. This is known as 'paedomorphosis'. Conversely, if the

descendant undergoes greater development, it is said to show 'peramorphosis'. These are descriptive terms that portray the descendant morphological pattern. Each of these two phenomena can be generated by three different processes. Paedomorphic morphologies occur if the duration of growth of the descendant form is prematurely truncated (progenesis), if the actual growth rate is less in the descendant than in the ancestor (neoteny), or if onset of growth is delayed (postdisplacement). Progenesis can often affect the whole organism if onset of sexual maturity occurs prematurely, or it may involve only certain traits. Neoteny and postdisplacement generally affect only certain traits, not the entire organism.

Conversely, peramorphic morphologies occur if duration of growth in the descendant is extended (hypermorphosis), if the actual growth rate is increased in the descendant (acceleration), or if onset of growth is earlier in the descendant (predisplacement). Hypermorphosis can affect the whole organism if onset of sexual maturity is delayed, or it can target just certain traits. Acceleration and predisplacement affect only certain traits, not the entire organism.

Heterochronic terminology can be applied both to the appearance during ontogeny of meristic characters (in other words, discrete structures formed during ontogeny, such as the number of spines in an echinoid) or to the subsequent changes in shape of these traits. These are called 'mitotic' and 'growth' heterochrony, respectively (McKinney and McNamara 1991). In many organisms (animals in particular) mitotic heterochrony, induced especially by predisplacement and postdisplacement, can be important very early in development. This is because variations can occur between ancestors and descendants in the timing of onset of development of major morphological features. Neoteny and acceleration will be particularly influential during subsequent ontogenetic development. Progenesis and hypermorphosis frequently come into play at a late stage in ontogeny, as they reflect variations in the time of offset of growth.

Heterochrony and allometry

As most organisms grow they not only increase in size, but also change shape. This relationship between size and shape is known as 'allometry'. If during ontogeny the relative size and shape of a structure remains the same, relative to overall body size, growth is said to be isometric. In reality few, if any, organisms are known to grow isometrically (Klingenberg 1998). Generally during ontogeny a particular structure will change shape and size relative to the size and shape of the entire organism. If there is an increase in size, growth is said to occur by 'positive allometry'. Conversely, if there is a relative decrease in size, growth is said to show 'negative allometry'. Heterochrony involves changes not only in time, but also in shape and size. Consequently there is a close relationship between allometry and heterochrony. The effect of changes to growth rates is to change allometries. Increase in allometry is expressed phylogenetically as peramorphosis, whereas reducing it produces paedomorphosis. Extensions or contractions of the period of growth, i.e. hypermorphosis or progenesis, exacerbate or contract the effects of allometric changes. Consequently, those organisms that undergo pronounced allometric change during growth are more likely to generate very different descendant adult morphologies if rates or durations of growth are changed.

The classic example of this is the dog, *Canis familiaris*. By comparison with the domestic cat, *Felis domestica*, the dog skull undergoes pronounced positive allometric changes during ontogeny. Consequently, artificial tampering with growth rates and timing has produced a wide range of breeds that vary substantially in cranial morphology. By contrast, in the domestic cat, extent of allometric change is minimal, thus breeds do not vary greatly in morphology (Wayne 1986). In the natural world the same effect is produced. Organisms producing a wider range of variation because of greater inherent allometric change during ontogeny generate more raw material for natural selection to work on, leading potentially to the evolution of a wide range of descendants.

Heterochrony in fossils

Identifying heterochrony in the fossil record requires ontogenetic information about both ancestral and presumed descendant forms. Because two of the factors involved in heterochrony are usually available with fossil material, namely shape and size, it is often relatively easy to assess whether a particular species is either peramorphic or paedomorphic, or whether certain traits are peramorphic or paedomorphic. However, understanding which process or processes caused the heterochronic effect is more difficult. There has been a tendency to use size as a proxy for time. Thus assumptions are made that, for example, a descendant which is smaller than its ancestor, and shows paedomorphic morphological characteristics, ceased growing at an earlier age and therefore arose by progenesis. Examples described include Cambrian trilobites, such as *Olenelloides* (McKinney and McNamara 1991) (Fig. 2.3.5.1), Devonian ammonoids such as *Balvia* (Korn *in* McNamara 1995), and early Mesozoic urodele and anuran amphibians (Schoch *in* McNamara 1995) (Fig. 2.3.5.2). While in general terms this may often hold true, particularly at higher taxonomic levels, it may not always be the case. Thus care needs to be taken in assigning heterochronic processes to fossil material when age data are lacking (Jones *in* McKinney 1988). One way around the

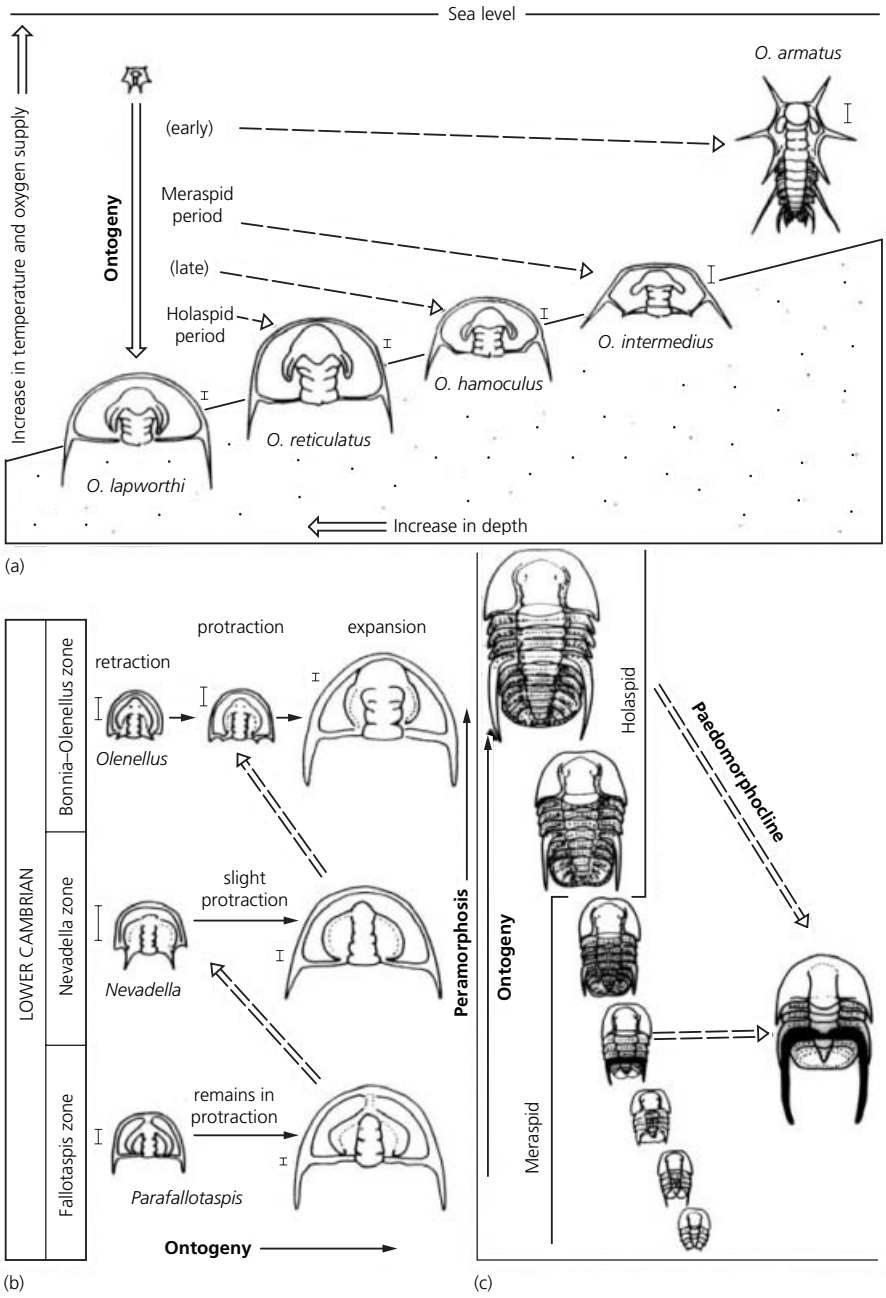

Fig. 2.3.5.1 Heterochrony in trilobites. (a) Paedomorphosis in Early Cambrian species of *Olenellus*; from the ancestral species, *O. lapworthi*, a number of species evolved showing different degrees of paedomorphosis. (b) Peramorphosis in Early Cambrian olenellids; successively younger species underwent greater morphological change during their ontogeny.(c) Paedomorphosis in Early Ordovician species of *Acanthopleurella*; the adult of the derived paedomorphic species has the same number of thoracic segments as a juvenile of the ancestor. (From Fortey and Owens *in* McNamara 1990.)

problem of the absence of direct time data in fossil material is to apply the term 'allometric' to the heterochronic process, such as 'allometric progenesis' (McKinney 1988). However, recent work on bone microstructure in dinosaurs, such as *Troodon* (Varricchio 1993), has revealed that seasonal growth is reflected in growth lines in the bone, showing that 'real' time information can sometimes be gleaned from appropriate fossil material. Moreover, the time of onset of maturity can be deduced. Given such information, more accurate assessments can be proposed of the likely activity of particular heterochronic processes in extinct species.

Theoretically paedomorphosis and peramorphosis should, in general terms, occur with approximately equal frequency (Gould 1977). However, studies of heterochrony in the fossil record show that this may not always be the case (McNamara *in* McKinney 1988). Organisms' development systems appear to have been poorly constrained in the Early Cambrian; this is particularly noticeable in trilobites (McNamara 1986), as demonstrated by their high levels of variability in segment number, both intraspecifically and interspecifically. Through the Cambrian there is progressive developmental hardening, such that by post-Cambrian

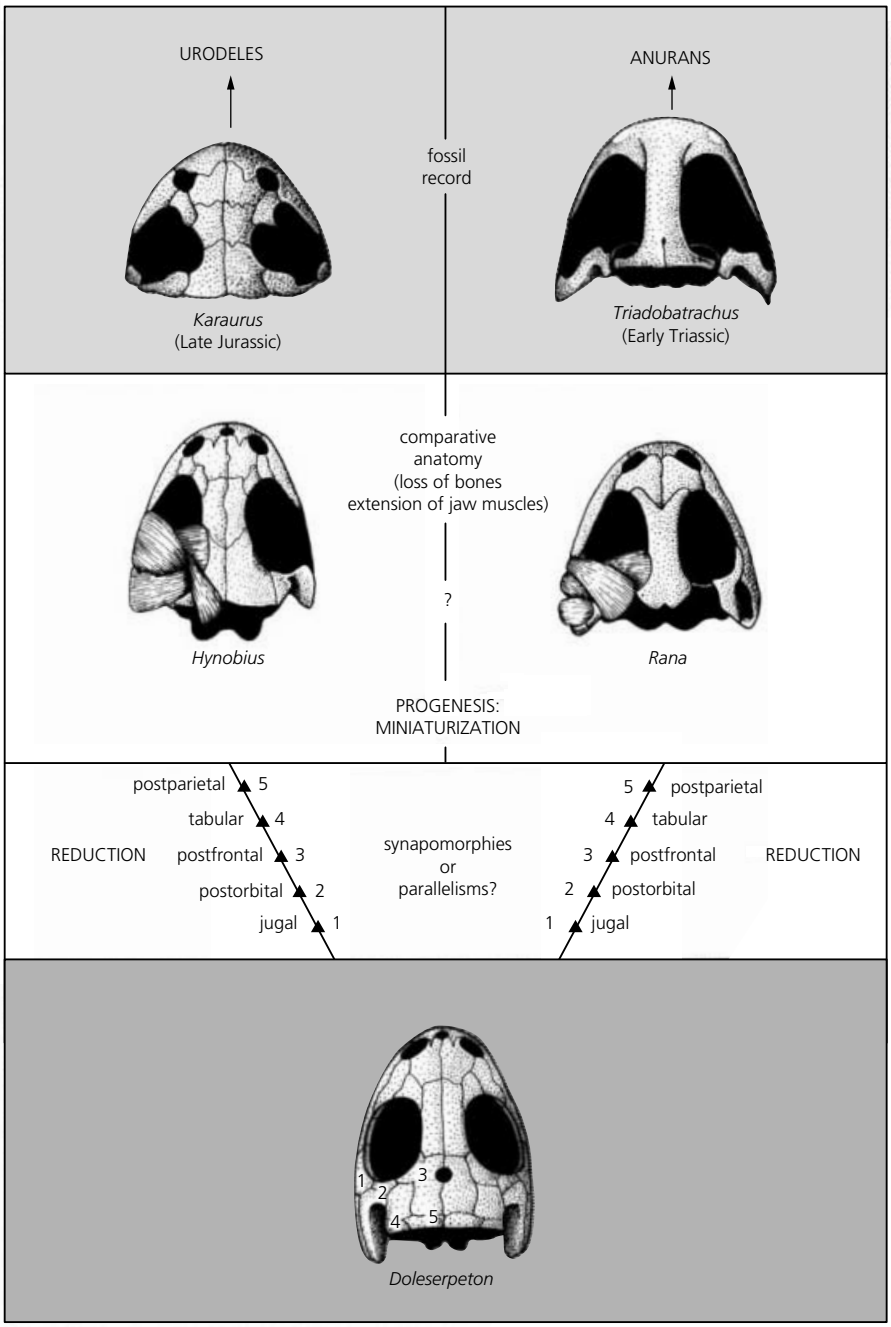

Fig. 2.3.5.2 Suggested evolution of urodeles (salamanders) and anurans (frogs) from a dissorophoid amphibian by progenesis. Features of the skull in these derived forms are much reduced by comparison with the ancestor. This shows the importance of progenesis in the evolution of major morphological novelties. (From Schoch *in* McNamara 1995.)

times many higher-level taxa show a fixed thoracic segment number. Moreover, documented cases indicate that in Cambrian trilobites natural selection favoured paedomorphic processes more than peramorphic ones. In contrast, the greater morphological diversity of post-Cambrian trilobite taxa has been ascribed to a shift to selection for predominantly peramorphic processes.

Heterochrony played a crucial role in dinosaur evolution (McNamara 1995). Here also, one type of heterochrony seems to have occurred more frequently. Many lineages, such as in sauropods, ceratopsians, theropods, and ornithopods, are characterized not only by trends towards increased body size, but also by the attainment of larger, more complex morphologies by peramorphosis (Fig. 2.3.5.3). Microstructure of dinosaur bone indicates that many juveniles experienced very rapid growth rates. From this it can be inferred that the peramorphic process acceleration played an important role in dinosaur evolution. Hypermorphosis may also have contributed to the attainment of a large body size.

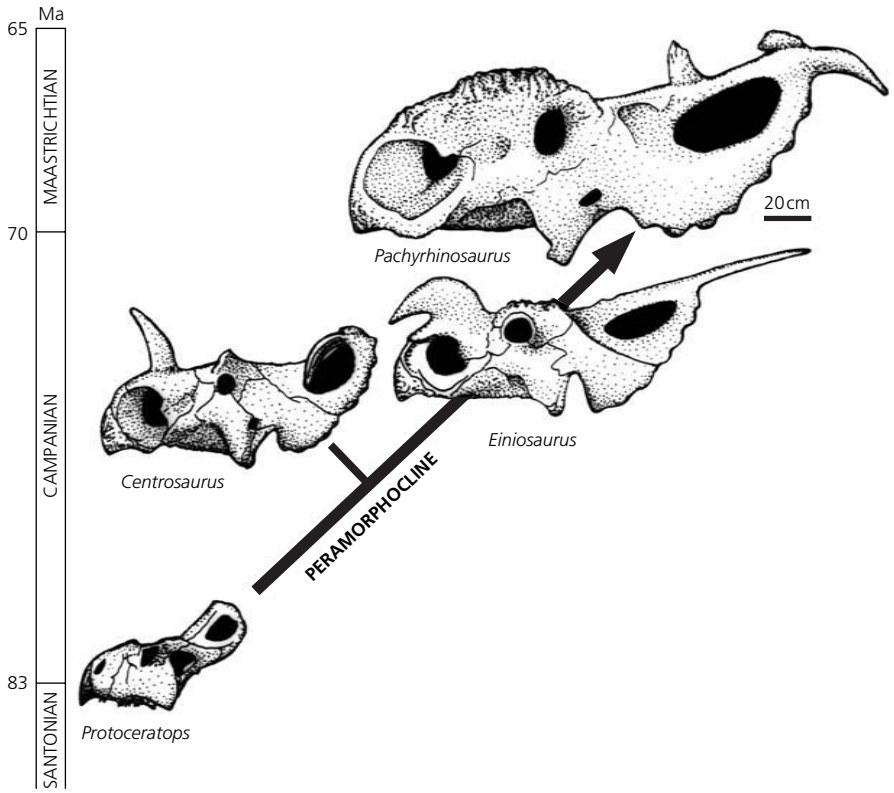

Fig. 2.3.5.3 Suggested peramorphic evolution of ceratopsian dinosaurs. Successively younger genera were large and evolved morphologically more complex horns on the skull. (Amended from McNamara and Long 1998.)

Dissociated heterochrony

The role of peramorphosis in generating increase in body size by either hypermorphosis or acceleration suggests that Cope's Rule (the trend of phylogenetic increase in body size) may have its origins in peramorphosis. Studies of lineages of Jurassic bivalves and ammonites (Hallam 1975) demonstrated that almost all showed trends to increased body size. Similar patterns are evident in foraminifers, primates, and other mammals (McKinney *in* McNamara 1990). One consequence of peramorphosis involving size increase is that it is often associated with paedomorphic trends in some traits. In other words, there has been dissociated heterochrony, where some morphological traits are peramorphic, while others are paedomorphic. Organisms are rarely all peramorphic or all paedomorphic. Peramorphic and paedomorphic traits may possibly be linked, in that paedomorphic traits may be developmental trade-offs for peramorphic features. Involving, as it does, increase in body mass, trends towards increased size mean that there has to be a greater input of energy to enable the organism to attain a larger body size, and often more complex morphological features, than its ancestor.

Classic examples of such trade-offs are found in dinosaurs, ratite birds, and hominids (McNamara 1997). For example, in tyrannosaurids the peramorphic trend of increased body size, in combination with increased complexity and size of the skull and hindlimbs, is offset by a paedomorphic reduction in the forelimbs. Similarly in large ratites, such as the ostrich and emu, trends to a large body size and very large hindlimbs are offset by a paedomorphic reduction in the wings and a flightless habit. In hominid evolution the trend has been for an increase in body size and peramorphic evolution of the brain and hindlimbs, both increasing in size and complexity. Developmental trade-offs, in particular for the larger brain, include a reduction in size of the gut. The brain is a metabolically hungry organ, and compared with all other primates our brain size is relatively much larger, while our guts are relatively smaller. This paedomorphic reduction in gut size and complexity was accompanied by a dietary change between species of *Australopithecus* and the descendant species of *Homo*. A smaller gut could cope with a diet of higher nutritional level, i.e. meat rather than just vegetation. Selection for a gut able to process such a higher protein diet meant that a paedomorphic reduction in jaw and tooth size and complexity was also possible.

Heterochrony and macroevolution

Heterochrony has long been invoked as the agent for the evolution of major evolutionary novelties. As early as the 1920s Walter Garstang suggested that paedomorpho-

sis resulted in the evolution of vertebrates from a tunicate-like larva. Of the paedomorphic processes, progenesis operating early in development has been thought a particularly important process in generating novel morphologies. For instance, the first clypeasteroid echinoids, which evolved in the Paleocene, were extremely small, resembling juvenile cassiduloid echinoids, from which it has been suggested they evolved. Likewise, the evolution of insects from a multisegmented ancestor, such as a euthycarcinoid, would have involved much earlier onset of maturation, resulting in a descendant adult retaining the ancestral early juvenile complement of only three pairs of thoracic appendages (McNamara 1997). In both instances, selection may have predominantly targeted the small body size, rather than any particular morphological attribute. A similar mechanism has been invoked for the evolution of anurans (frogs) and urodeles (salamanders) from advanced dissorophoid amphibians in the Early Triassic and Late Jurassic (Fig. 2.3.5.2), respectively (Schoch *in* McNamara 1995). In both of these more modern forms of amphibians, features of the skull are much reduced and less complex than in early amphibians. However, here also small size might have been a target of selection in the environment at a time of increasing aridity.

The loss of limbs in snakes and in whales is another example of the importance of paedomorphosis in the evolution of morphological novelties, but here, rather than progenesis, the process is more likely to have been neoteny or postdisplacement, or a combination of the two. The seeming preponderance of paedomorphosis as an instigator of morphological novelties that lead to the evolution of major new taxa is a function, in part, of the greater morphological difference between very early embryonic and adult forms, compared with adult morphologies that have been accelerated or extended by hypermorphosis. However, it is possible that peramorphic changes very early in development, such as the earlier induction of specific morphological traits, might play just as important a role in generating morphological novelties as paedomorphic delays. Thus changes to the timing of formation of structures, such as forelimb condensation, can profoundly affect the appearance of the resultant adult form.

Heterochrony and evolutionary trends

Heterochrony also plays an important role in evolutionary trends. These trends can be either anagenetic or cladogenetic, and within or between species (McNamara 1990). The relationship between evolutionary trends and heterochrony arises because, by their very definition, trends are unidirectional, in much the same way as are ontogenetic trajectories. However, for trends to develop, extrinsic factors are also critical, in addition to the intrinsic factor of heterochrony. Selection of either progressively more paedomorphic or more peramorphic traits must take place along an environmental gradient, such as in the aquatic environment from deep to shallow water, or from coarse to fine-grained sediment substrates.

An evolutionary trend from ancestors to descendants that show increasingly more paedomorphic characters is called a 'paedomorphocline'. If the trend shows increasing peramorphic descendants it is called a 'peramorphocline' (McNamara 1990). Collectively these are called heterochronoclines (McKinney and McNamara 1991). The driving force behind heterochronoclines is often competition or predation pressure. With the induction of a heterochronocline by competition the persistence of the ancestral form constrains selection to one direction, along an environmental gradient away from the ancestral species. The resultant phylogenetic pattern is one of cladogenesis. Selection caused by predation pressure induces an anagenetic heterochronocline. Such trends have been described in taxa such as spatangoid echinoids, where predation pressure has resulted in heterochronoclines evolving along an environmental

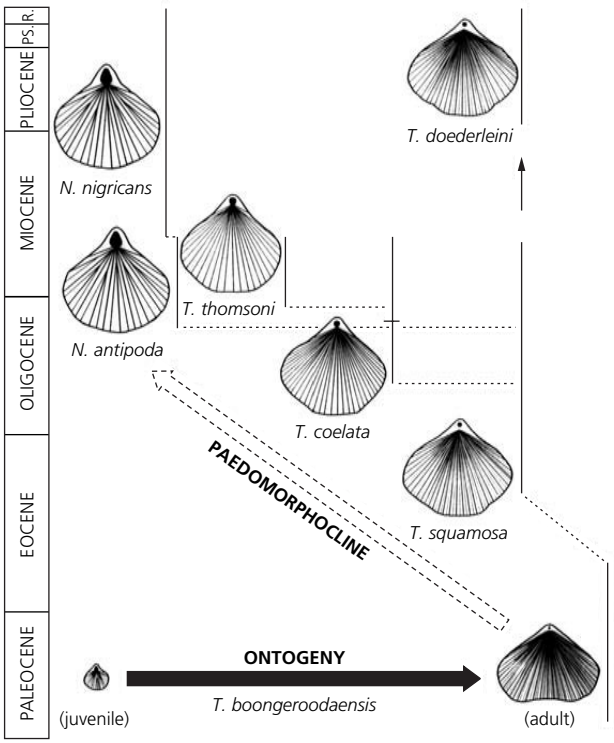

Fig. 2.3.5.4 Paedomorphocline in the rhynchonellid brachiopods *Tegulorhynchia* and *Notosaria*. The older species lived in deeper water than younger species. Paedomorphosis resulted in the evolution of characters in the descendants that enabled colonization of a higher energy environment in shallow water. (From McNamara 1990.)

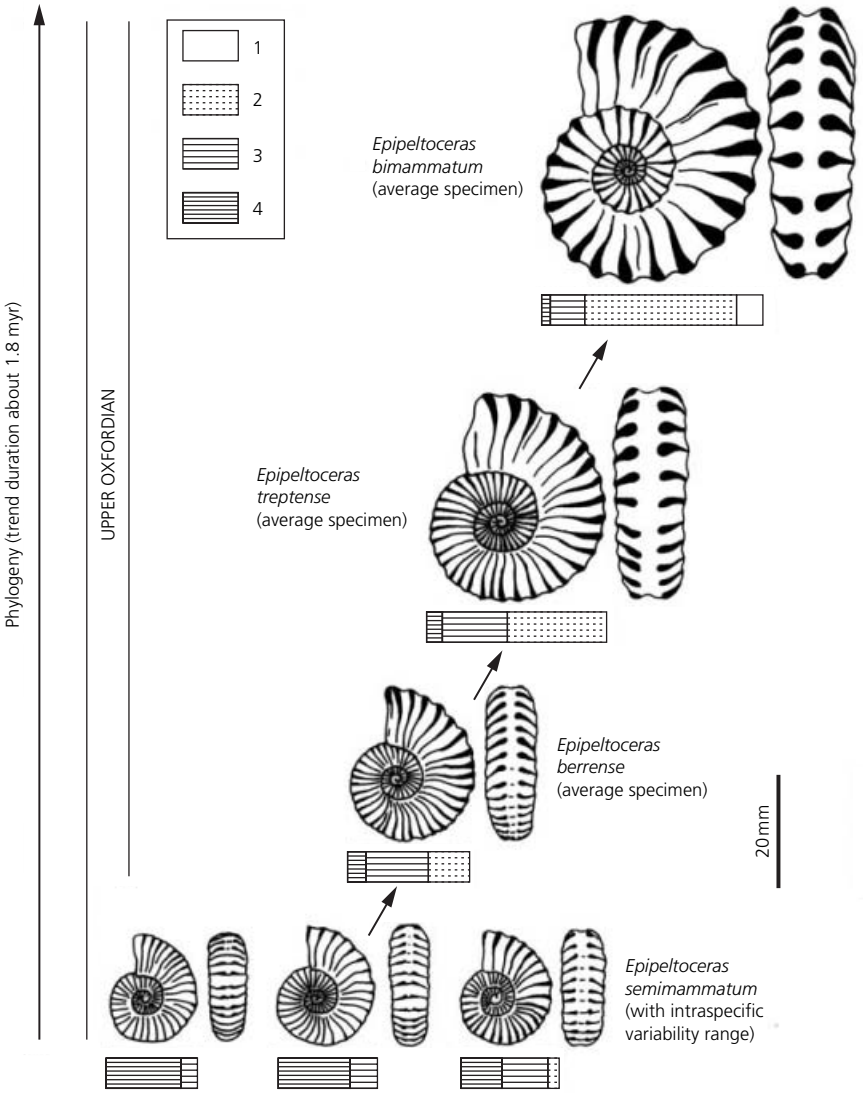

Fig. 2.3.5.5 Peramorphocline in the Jurassic ammonite *Epipeltoceras*; rapid evolutionary change by extending the extent of growth producing a more complex and larger shell. 1 represents stout ornamentation of ribs terminated by such coarse and prominent lateroventral tubercles that the smooth ventral area seems depressed. 2 represents the same, but with less bold ornamentation. 3 represents continuous ribs that only weaken on the ventral area. 4 represents slender ornamentation comprising ribs crossing the regularly rounded ventral area without interruption or weakening. (From Dommergues *in* McNamara 1990.)

gradient from coarse to fine-grained sediments, reflecting, perhaps, shallow to deep water (McNamara 1997). An example of a cladogenetic paedomorphocline is the Cenozoic brachiopod lineage of *Tegulorhynchia–Notosaria* (McKinney and McNamara 1991), which developed along an environmental gradient of deep to shallow water (Fig. 2.3.5.4). Many examples of heterochronoclines have been described in ammonoids (Fig. 2.3.5.5) (Dommergues *in* McNamara 1990; Korn *in* McNamara 1995).

Heterochrony and life history

A close relationship exists between heterochrony and life history strategies (McNamara 1997). These include factors such as size at birth, growth rates, age at maturation, body size at maturity, the number, size, and sex of offspring, and length of life. Many of these are determined by heterochrony. Attempts to categorize life history traits have been of limited success. The most widely known is the '*r–K* continuum', a descriptor of environments and the life history traits of their inhabitants. While the *r–K* continuum is an oversimplification of life history strategies in general, it does seem to work at higher taxonomic levels.

The *r*-selected extreme is a categorization of unpredictable, often ephemeral environments. Selection pressure for organisms inhabiting such environments targets those that mature rapidly, have short life spans, and are small in size. These are traits produced by progenesis. Such organisms typically produce large numbers of offspring. At the other extreme are *K*-selected populations, inhabiting constant, predictable environments. Characteristic features of organisms inhabiting such environ-

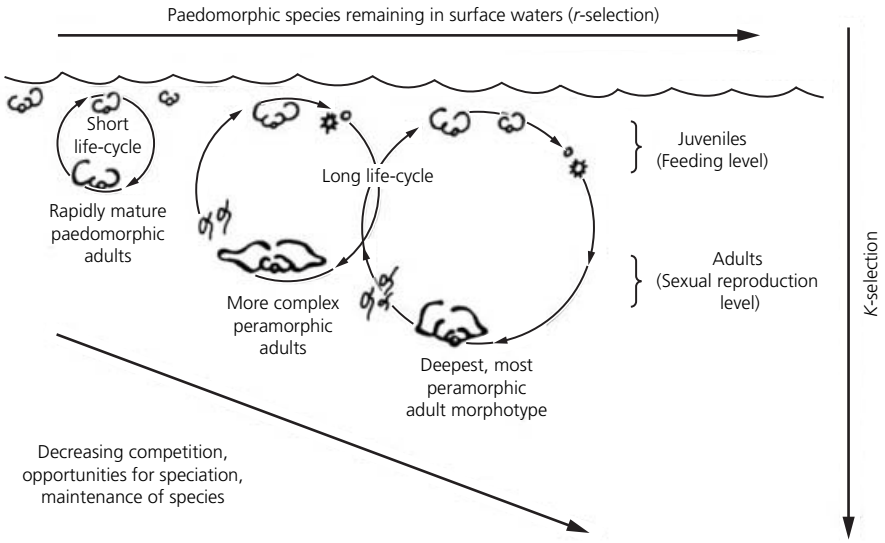
Paedomorphic species remaining in surface waters (r-selection)
Short life-cycle
Rapidly mature paedomorphic adults
Long life-cycle
Juveniles (Feeding level)
Adults (Sexual reproduction level)
More complex peramorphic adults
Deepest, most peramorphic adult morphotype
K-selection
Decreasing competition, opportunities for speciation, maintenance of species

Fig. 2.3.5.6 Relationship between heterochrony and life history in planktic foraminifers. In less stable, shallow-water environments the foraminifers attain sexual maturity and cease to grow earlier than in deeper-water forms. (After Caron and Homewood 1983.)

ments are delayed onset of reproduction, long life span, and large body size, all traits typical of hypermorphosis. These organisms produce few, large offspring.

As well as being produced by progenesis, *r*-selected characteristics may also be produced by acceleration. Conversely, many *K*-selected organisms appear to show some traits that evolved by neoteny, as well as hypermorphosis. It is probably for this reason that these two pairs of processes often go together. Assessment of heterochronic patterns in the fossil record can sometimes allow judgements to be made of the life history strategies of extinct organisms. Particularly interesting examples have been described in foraminifers (Caron and Homewood 1983). During periods of environmental stress paedomorphic planktic foraminiferal species invade the oceanic surface waters. This is an *r*-selected environment. Deeper-water species show *K*-selected features: longer life cycles and relatively hypermorphic, larger, and more complex morphologies. During periods of high sea level the ocean depth on the shelf is greater and more *K*-selected hypermorphic species occur in this more stable environment. Conversely, with a drop in sea level, opportunistic, progenetic taxa invade the more unstable, stressful environment (Fig. 2.3.5.6).

Heterochrony can affect life history traits in other ways. Many organisms undergo pronounced morphological, behavioural, and ecological changes during ontogeny, such as the transition of amphibians from a juvenile, aquatic environment to an adult, terrestrial, air-breathing environment. Changes in the timing of transition from one phase to another (called sequential heterochrony) can cause significant morphological and behavioural changes to the descendant adult. For example, in the living axolotl (*Ambystoma mexicanum*) the juvenile phase has been extended for so long that sexual maturity occurs and metamorphosis is inhibited. Such morphs appear as paedomorphic forms that spend their entire lives in the aquatic environment. This is not, as frequently cited in the literature, neoteny, as there has been no reduction in growth rate, but an example of sequential hypermorphosis.

Heterochrony thus plays a central role in evolution. It provides the raw material for natural selection to work on and operates from the intraspecific to the highest taxonomic levels. Heterochrony, genetics, and natural selection form the evolutionary triumvirate.

References

Caron, M. and Homewood, P. (1983) Evolution of early planktic foraminifers. *Marine Micropalaeontology* **7**, 453–462.

Gould, S.J. (1977) *Ontogeny and phylogeny*. Belknap, Cambridge, Massachusetts.

Hallam, A. (1975) Evolutionary size increase and longevity in Jurassic bivalves and ammonites. *Nature* **258**, 493–497.

Klingenberg, C.P. (1998) Heterochrony and allometry: the analysis of evolutionary change in ontogeny. *Biological Reviews* **73**, 79–123.

McKinney, M.L., ed. (1988) *Heterochrony in evolution: a multidisciplinary approach*. Plenum, New York.

McKinney, M.L. and McNamara, K.J. (1991) *Heterochrony: the evolution of ontogeny*. Plenum, New York.

McNamara, K.J. (1986) The role of heterochrony in the evolution of Cambrian trilobites. *Biological Reviews* **61**, 121–156.

McNamara, K.J., ed. (1990) *Evolutionary trends*. Belhaven, London.

McNamara, K.J., ed. (1995) *Evolutionary change and heterochrony*. Wiley, Chichester and New York.

McNamara, K.J. (1997) *Shapes of time: the evolution of growth and development*. Johns Hopkins University, Baltimore.

McNamara, K.J. and Long, J.A. (1998) *The evolution revolution*. Wiley, Chichester and New York.

Varricchio, D.J. (1993) Bone microstructure of the Upper Cretaceous theropod *Troodon formosus*. *Journal of Vertebrate Paleontology* **13**, 99–104.

Wayne, R.K. (1986) Cranial morphology of domestic and wild canids: the influence of development on morphological change. *Evolution* **40**, 243–261.

2.3.6 Hierarchies in Evolution

T.A. GRANTHAM

Introduction

The biotic world is hierarchically organized. Organisms are composed of organ systems, which are composed of tissues; tissues are composed of cells, which in turn are composed of organelles. At the other end of the spectrum, sexual organisms are clustered into local breeding populations, species are groups of populations, and higher taxa are groups of species. While these observations are almost trivial, the scientific, philosophical, and methodological problems of understanding hierarchical systems are anything but trivial. Two clusters of problems seem particularly pressing.

1 Problems of ontology: what status should we give to entities at different levels? That is, must we recognize higher-level entities—demes, species, and higher taxa—as 'individuals'? Do higher-level entities possess 'emergent' properties? How are emergent properties possible if higher-level entities are simply aggregates of lower-level entities? (See Hull 1980 and Vrba 1989 for more on individuality and emergence, respectively.)

2 Problems of methodology: assuming that processes at the level of interest can be influenced by events at adjacent levels, what methods will allow us to disentangle the web of causal influences that flow across hierarchical levels? For example, when should differences in species durations be attributed to selection at the species level rather than selection at lower levels?

Ecological and genealogical hierarchies: theme and variations

It is tempting to think of the living world as a single hierarchical system ranging from biomolecules to the biosphere. However, contemporary evolutionary theorists insist that evolution should be understood as the interaction of two distinct hierarchies: an ecological hierarchy and a genealogical hierarchy. There are three principal ways of conceptualizing these hierarchies:

1 Eldredge (1989) argued that evolutionary theory must be concerned with at least two distinct hierarchies (Fig. 2.3.6.1). First, because of our interest in phylogeny, evolutionists are concerned with genealogical hierarchies. For Eldredge, genealogical entities are defined (and connected) by their reproductive activity. Organismic reproduction gives rise to local breeding populations (demes). The reproduction of demes leads to a set of potentially interbreeding populations (i.e. a species); and the reproduction of species (i.e. speciation) generates monophyletic clades. Despite some obvious similarities, Eldredge believes that the genealogical hierarchy should be distinguished from the Linnaean hierarchy. Palaeobiologists' interest in ecological relations (e.g. the evolution of community structure) leads them to consider a second hierarchy: avatars (a localized group of conspecific organisms viewed as parts of an ecological community, which may or may not be identical to the genealogical deme), communities, regional biotas, etc. The ecological hierarchy can be conceived in two distinct ways: some view populations as parts of ecosystems that include the abiotic realm, while others emphasize a more narrowly biotic conception of communities. Since organismic interactions with the biotic and abiotic environment can influence reproductive success, evolutionary

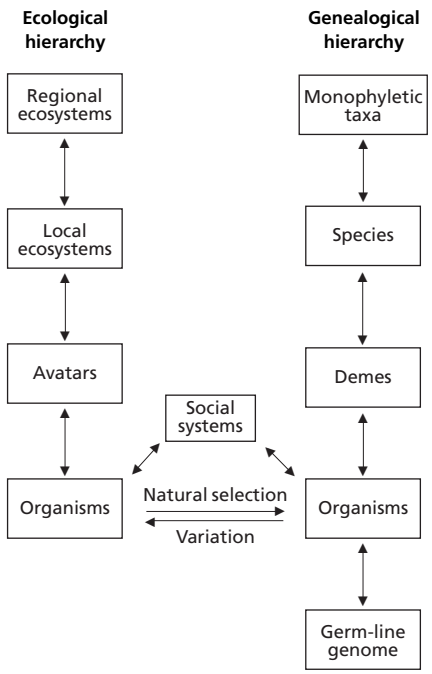

Fig. 2.3.6.1 Ecological and genealogical hierarchies. According to Eldredge, evolutionary theory should emphasize two distinct but interacting hierarchies. Entities at any given level of a hierarchy can be influenced by processes at both lower and higher levels in that hierarchy. Interactions between the hierarchies occur primarily through individuals and social groups. (From Eldredge and Greene 1992; reprinted with permission.)

theory must strive to understand the interactions between the genealogical and ecological hierarchies.

2 In a similar vein, philosophers of biology have identified two hierarchies in evolution: a hierarchy of 'replicators' and a hierarchy of 'interactors' (Hull 1980; Brandon 1990). Replicators and interactors are defined as entities that function in selection processes. A replicator 'passes on its structure largely intact in successive replications', while an interactor 'interacts as a cohesive whole with its environment in such a way that interaction causes replication to be differential' (Hull 1980, p. 96). The philosophical account resembles Eldredge's approach because replicators are fundamentally genealogical entities and interactors are fundamentally ecological entities. None the less, these approaches differ in important ways. The most basic difference is that interactors and replicators are defined with respect to selection processes whereas Eldredge's concepts are not. Because the philosophical account is concerned with one form of environmental interaction (i.e. interactions that influence replication), some members of Eldredge's ecological hierarchy (e.g. communities) almost certainly do not function as interactors (see Table 2.3.6.1).

3 Williams (1992) offers a third way of conceptualizing the hierarchies of evolution based on his distinction between the material and codical domains of evolution. The codical domain is concerned with the information encoded in genes, genotypes, and gene pools. Like replicators, these entities (which Williams calls 'codices') are defined in terms of their ability to preserve and pass on information. However, Hull's replicators are material entities that pass on a physical structure, whereas Williams' codices are immaterial. For Williams, the (codical) gene is fundamentally a bit of information that can be carried in several different media (e.g. DNA, RNA, protein). This information must, of course, occur in some medium; but selection in the codical domain concerns the information, not the material carriers of the information. Williams' emphasis on the (immaterial) codical domain distinguishes his view from both Hull's and Eldredge's accounts. Selection in the material domain concerns material entities (which Williams calls interactors). In his view, selection in the material domain can occur at virtually any level from molecules to higher taxa. Selection in the material domain is, then, similar to Hull's analysis of selection among interactors. However, since Williams believes that selection at the level of clades is conceivable, he is committed to the claim that genealogically defined higher taxa can function as ecological interactors—something both Hull and Eldredge question.

Distinguishing selection and sorting in hierarchical systems

Early advocates of the hierarchical expansion of Darwinism suggested that any difference in speciation and/or extinction rates was evidence of species selection. Vrba and Gould (1986) criticized this view and argued that sorting (i.e. differential survival and reproduction) is crucially different from selection. Suppose, for example, that tall primroses have greater reproductive success than shorter forms. This difference might arise in any number of ways, for example: (a) tall individuals (by chance) occupy more favourable soil and light conditions; (b) height provides some advantage in the struggle for survival; or (c) the genes for height are linked to genes that provide some advantage in the struggle for survival. While all three cases involve sorting by height (a correlation between height and reproductive success), only (b) involves selection for height. Thus, if terms are to be used consistently across levels of the biological hierarchy, species selection should not be equated with species sorting; selection is only one possible explanation of sorting (see Vrba and Gould 1986; Vrba 1989).

What criteria can we use to determine when selection is acting at a given level? According to Lewontin's (1970) influential analysis, selection requires heritable variation

Table 2.3.6.1 Hierarchies of interactors and replicators. According to Hull (1980) and Brandon (1990), the selection scenario determines which entities function as replicators and interactors. Thus, these hierarchies are process-specific; they concern entities that enter into the selection process. (From Brandon 1990; reprinted with permission.)

Selection scenario	Interactor	Replicator
Origins of life	lengths of RNA	lengths of RNA
'Selfish genes'	lengths of DNA	lengths of DNA
Meiotic drive	(part of) chromosome	(part of) chromosome
Somatic selection	parts of organisms	genes or genome
Organismic selection:		
asexual reproduction	organism	genome (or organism?)
sexual reproduction	organism	genes
Intrademic group	group	genes
Interdemic group	group	group
Avatar selection	avatar	avatar
Species selection	species	species
Clade selection	clade	clade

in traits that influence fitness. Thus, selection occurs at any level (from genes on up) when entities at that level vary in heritable traits that affect the likelihood of surviving or reproducing. While virtually all philosophers and biologists accept heritable variation in fitness as necessary for selection, many maintain that Lewontin's conditions are not sufficient. The problem is that even if a (heritable) group-level trait varies and influences group-level fitness, group-level differences may be a simple result of differences at the organismic level. That is, the group selection explanation may be reducible. To cite a familiar case, the fact that fleet-footed herds of deer survive longer than slow herds is evidence for group selection only if the differences in group survival cannot be fully explained as a result of organismic selection for fast deer. Much of the philosophical (non-empirical) debate over units of selection has attempted to solve this problem (see Sober and Wilson 1994).

The standard strategy for improving Lewontin's analysis is to add an additional requirement. One influential proposal stipulates that selection at a level requires traits that are emergent at that level (Vrba 1989). According to this approach, species selection occurs if and only if variation in heritable and emergent species-level traits causes variation in species-level fitness. This position hinges on the distinction between aggregate and emergent traits. Aggregate traits are 'sum of the parts' traits—they are attributed to a higher-level entity simply because the parts of the larger entity have that trait. For example, if the organisms of a species are generalists, then the species has an aggregate property of being a 'generalist species'. By contrast, emergent traits cannot be attributed to entities at lower levels. For instance, population structure is considered an emergent trait because organisms do not have population structure. (Degree of morphological variability and geographical range are also considered emergent species-level traits.) Vrba argues that emergence is a necessary condition for selection because: (1) higher-level selection should be recognized as a truly distinct evolutionary force only if it can oppose lower-level selection; and (2) higher-level selection cannot oppose lower-level selection unless it is acting on emergent traits.

Vrba's approach has been criticized for being too restrictive. In particular, evolutionary theorists have suggested that species selection can occur without emergent species-level properties (e.g. Lloyd 1988). This claim is generally defended by analysing mathematical models of selection. According to Lloyd (and others), mathematical models of evolution use trait-fitness covariation to represent selection. As a result, they claim that a selection explanation is irreducible exactly if the covariation between a trait and a component of fitness at the level of interest cannot be represented as the covariation of traits and components of fitness at lower levels. Because emergent traits cannot be represented at lower levels (this is roughly the definition of an emergent trait), the presence of an emergent trait guarantees that the trait-fitness correlation is irreducible. None the less, Lloyd maintains that emergent traits are not strictly necessary for species selection: an irreducible component of fitness would also ensure that the trait-fitness covariation cannot be represented at lower levels. That is, if differences in an aggregate species-level trait cause differences in an irreducible component of species-level fitness, then this explanation is irreducible and should count as an instance of species selection (see Grantham 1995).

Concerns about higher-level selection

Although few biologists question the conceptual possibility of species selection, only a few cases of species selection have survived critical scrutiny. G.C. Williams—a self-proclaimed reductionist who has, historically, been no friend to hierarchical approaches—captures the current mood when he claims that there can be 'no question of the reality of [species and] clade selection . . . The important issues relate to its exact nature and importance' (Williams 1992, p. 50). There are, none the less, a number of pressing concerns about species selection and selection of higher taxa. First, only a few emergent species-level characters appear to be evolutionarily significant (e.g. geographical range, variability, mating systems). If species selection does require emergent species-level character variation, then the significance of species selection will be limited by the paucity of truly emergent characters. (If palaeontologists adopt Vrba's definition of species selection, it will be important to continue to refine the concept of emergence.) A second objection is that, because organisms have a short generation time relative to species, organismic selection within the lifetime of a species will exert greater influence on trends than species selection. This argument tends to assume, however, that species selection models aim to explain changes in organismic phenotypes; it has less force where species selection models are used to explain taxic trends (changes in the frequency of species-level traits within a clade). A third and more basic objection maintains that species are not cohesive enough to count as interactors. Except in those rare cases where a species exists as a single avatar, species are not (speaking strictly) ecological units and hence cannot be interactors. Furthermore, since the species of a clade generally do not share a common environment, it is improper to say that species are being selected for their adaptedness to a common environment (Damuth 1985). This third objection turns on a subtle confusion about the notion of the species-level selective environment (see Grantham 1995). Finally, given the small number of well-

documented examples, some critics argue that species selection is not a powerful force in macroevolution.

A number of biologists have recently entertained the possibility of selection occurring at the level of genera or even families (e.g. Williams 1992). According to Eldredge (1989), the selection of higher taxa is simply not possible because higher taxa do not (speaking strictly) reproduce. Although a species may be said to reproduce, one monophyletic clade cannot give rise to a distinct monophyletic clade.

Three positions on the significance of hierarchy

1 At the simplest level, hierarchical approaches require an examination of patterns of evolution at different levels, i.e. it cannot simply be assumed that the patterns of evolution remain constant across hierarchical levels. For example, studies of the selectivity of extinctions (see Section 2.3.9) and the onshore/offshore gradient in emergence of higher taxa of marine species (see Section 2.3.1) demonstrate that different patterns emerge at different levels. This is essentially a methodological point: palaeobiologists need to examine phenomena at different levels in order to adequately document the patterns of evolution. The recognition that evolutionary patterns vary across hierarchical levels does not, however, imply that higher-level properties or processes are causally significant.

2 The next step in advancing the concept of hierarchy is to recognize the possibility of causal interaction across levels. Perhaps the simplest form of interaction across levels is the 'effect hypothesis'. According to this hypothesis, selection on organismic traits can produce patterns of differential speciation and extinction. For example, there is considerable evidence that organism-level differences in feeding behaviour caused patterns of taxonomic diversification among African mammals (Vrba 1989). Because specialized feeders are dependent on a smaller range of food sources, they are subject to strong selection pressures as their food sources move, evolve, or go extinct. Species of specialized feeders display higher speciation and extinction rates than generalist species. The difference in speciation and extinction rates can, in turn, generate clade-level trends. This model of 'upward causation' goes beyond recognizing the existence of multiple hierarchical levels by incorporating the idea that speciation and extinction rates can influence clade-level trends. None the less, upward causation models retain an element of reductionism: macroevolutionary patterns are ultimately driven by lower-level causal processes.

3 More robust conceptions of hierarchy treat emergent properties and/or higher-level processes (e.g. species selection) as causally significant factors in evolution. For example, there is considerable evidence that some heritable and emergent species-level properties (e.g. geographical range) influence species-level fitness (Jablonski 1986). This kind of species selection explanation is robustly hierarchical: it requires both an ontological commitment to the reality of higher-level entities and a fully hierarchical explanatory framework. In contrast to the modern synthesis and Vrba's effect hypothesis—both of which treat higher-level properties and events as mere side-effects of lower-level processes—species selection explanations invoke higher-level properties as essential elements of the causal theory of evolution. In a robustly hierarchical system, both upward and downward causation occur. According to advocates of this more robust account, the unidirectional causal flow of traditional evolutionary biology (which treats macroevolution as a mere epiphenomenon) should be replaced by a theory in which events at both higher and lower levels can influence events at the level of interest.

While the notion of upward causation has become well entrenched, the robust conception of hierarchy remains controversial in some quarters. Critics of hierarchy point to conceptual and philosophical worries about the adequacy of central notions (emergence, species selection) as well as the dearth of empirical work demonstrating the causal significance of higher-level properties. Answering the critics will require the development of methodologies to distinguish among possible causes of macroevolutionary patterns, without simply assuming the superiority of either higher- or lower-level explanations. Lieberman's (1995) argument that phylogenetic analysis is important in assessing species selection explanations, for instance, is a significant step toward more rigorous tests of hierarchical explanations. While there is compelling evidence that species selection can and does occur, only further palaeontological research will determine how significant higher-level processes have been in the history of life.

References

Brandon, R.N. (1990) *Adaptation and environment*. Princeton University Press, Princeton, New Jersey.

Damuth, J. (1985) Selection among 'species': a formulation in terms of natural functional units. *Evolution* **39**, 407–430.

Eldredge, N. (1989) *Macroevolutionary dynamics*. McGraw-Hill, New York.

Eldredge, N. and Greene, M. (1992) *Interactions: the biological context of social systems*. Columbia University Press, New York.

Grantham, T.A. (1995) Hierarchical approaches to macroevolution: recent work on species selection and the effect hypothesis. *Annual Review of Ecology and Systematics* **26**, 301–326.

Hull, D.L. (1980) Selection and individuality. *Annual Review of Ecology and Systematics* **11**, 311–332. (Reprinted in D.L. Hull. 1989. *The metaphysics of evolution*. State University of New York Press, Albany, New York.)

Jablonski, D. (1986) Larval ecology and macroevolution in marine invertebrates. *Bulletin of Marine Science* **39**, 565–587.
Lewontin, R.C. (1970) The units of selection. *Annual Review of Ecology and Systematics* **1**, 1–18.
Lieberman, B. (1995) Phylogenetic trends and speciation: analyzing macroevolutionary processes and levels of selection. In: D.H. Erwin and R.L. Anstey, eds. *New approaches to speciation in the fossil record*, pp. 316–337. Columbia University Press, New York.
Lloyd, E.A. (1988) *Structure and confirmation of evolutionary theory*. Greenwood Press, New York.
Sober, E. and Wilson, D.S. (1994) A critical review of philosophical work on the units of selection problem. *Philosophy of Science* **61**, 534–555.
Vrba, E.S. (1989) Levels of selection and sorting with special reference to the species level. *Oxford Surveys in Evolutionary Biology* **6**, 111–168.
Vrba, E.S. and Gould, S.J. (1986) The hierarchical expansion of sorting and selection: sorting and selection cannot be equated. *Paleobiology* **10**, 146–171.
Williams, G.C. (1992) *Natural selection: domains, levels, and challenges*. Oxford University Press, New York.

2.3.7 Phylogenetic Tree Shape

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Introduction

The process of evolution by common descent means that groups of related species can be depicted as branching and sub-branching from one another like the limbs of a tree. In such a 'phylogenetic tree', the terminal branches may represent living or extinct species and internal branches represent the lines of ancestry that link them together. Just like real trees, phylogenetic trees may have a variety of shapes that reflect the processes that generated them.

Questions of tree shape have long been of interest to palaeontologists dealing with stratigraphic data. More recently this has been matched by an explosion of interest among biological systematists (see Mooers and Heard 1997). Most of the issues of tree shape are relevant in both of these traditions, but to discuss them it is necessary to make a basic distinction between the two broad categories of trees, stratigraphic phylogenies and cladograms.

Categories of tree

A stratigraphic phylogeny is one in which an axis represents geological time or stratigraphic level. Generally, such diagrams are constructed by palaeontologists for whom the starting point of an investigation is the systematic collection of fossils and the determination of the stratigraphic ranges of the taxa involved. How do palaeontologists decide which taxa are ancestral to which? One way is to use established cladistic methods. Another way is to infer ancestry from the existence of morphologically intermediate fossils at particular stratigraphic levels. This approach is sometimes called 'stratophenetics'. An important feature of most stratigraphic phylogenies is that they have a 'budding' configuration, in which 'ancestral' taxa persist through splitting events to coexist with their 'descendants' (Figs 2.3.7.1–2.3.7.3).

A cladogram is the output from a formal analysis of the character distributions or gene sequences in a group of related species. Cladograms have an equally splitting or 'bifurcating' configuration, which depicts the historical branching pattern most likely to have produced the observed character distribution (Figs 2.3.7.4 and 2.3.7.5). Time itself is not represented, although a cladogram may be 'calibrated' against the fossil record. Cladograms are

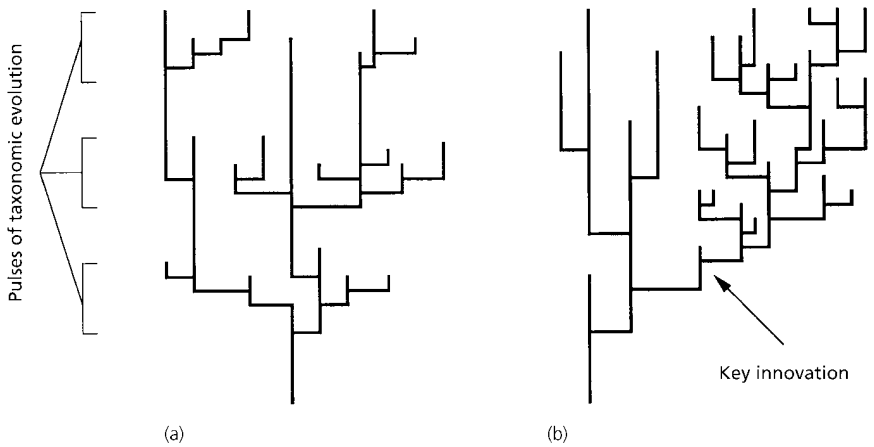

Fig. 2.3.7.1 Two ways in which stratigraphic phylogenies can deviate from random shapes. (a) The rate of taxonomic evolution (speciation and extinction) is not constant in time. (b) The rate of taxonomic evolution varies from one part of the tree to another.

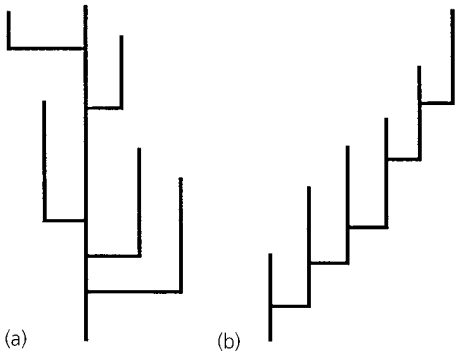

Fig. 2.3.7.2 Two patterns of phylogenetic asymmetry. (a) Iterative evolution, in which one or a few taxa repeatedly give rise to other taxa and tend to outlive them. This is a likely pattern of evolution in groups that repeatedly evolve across barriers between relatively stable and unstable environments (e.g. from the deep sea on to shelf seas). (b) Step-series evolution, in which descendant taxa tend to outlive their ancestors and are more likely to speciate. This pattern could be produced by evolution along an environmental gradient (e.g. a continental coastline) or it could be due to the competitive interaction between ancestors and their more successful descendants.

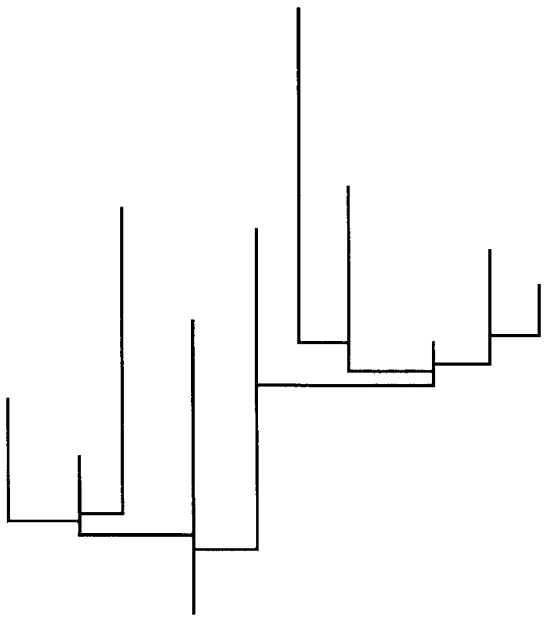

Fig. 2.3.7.3 Radiative evolution, in which internal branches are shorter than external (terminal) branches. This is one of the predictions of 'adaptive radiation'.

often constructed for living species only, in which case there is no place on them for extinct lineages even though they will have existed in most clades. Another important point is that all taxa necessarily plot out on terminal branches. This means that in cases where fossils are included in an analysis, the method will not identify

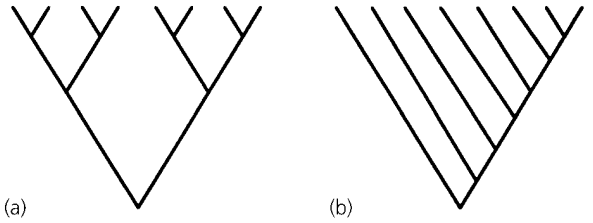

Fig. 2.3.7.4 Comparison between perfectly balanced (a) and imbalanced (b) cladograms. Balance is the extent to which internal nodes divide clades of equal size. Random branching patterns are neither very balanced nor imbalanced, but most cladograms tend to be more imbalanced than would be expected from a random model.

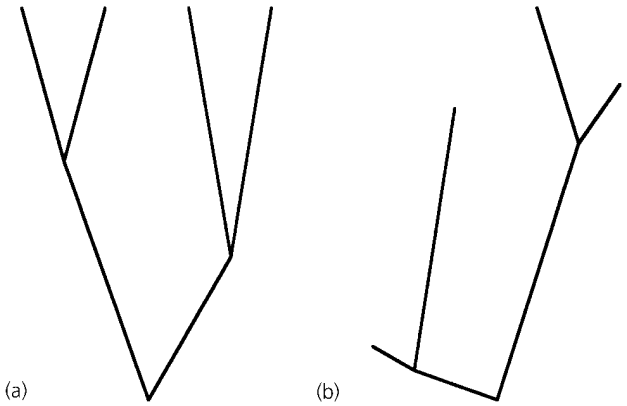

Fig. 2.3.7.5 Branch lengths can be made to represent the genetic distances between taxa. If substitutions occur at a roughly constant rate, branch lengths between related species pairs will be approximately equal (a). This means that if one divergence time is known, the others can be estimated assuming a molecular clock. Alternatively, rates of substitution may differ markedly between lineages (b) resulting in unequal branch lengths.

any species as ancestral to another, even if that were the case.

The importance of null models

Whatever sort of tree is analysed, the objective is to discern patterns that are unlikely to have arisen by stochastic processes (i.e. by chance). A useful null model to adopt therefore is one in which speciation and extinction probabilities are constant through time and across the tree (i.e. every event in the evolution of a group happened independently and entirely by chance).

Stratigraphic phylogenies

Temporal variation in speciation and extinction rates

If the rates of speciation and extinction vary in a system-

atic way in geological time, the tree that results is likely to be distinguishable from typical random trees. There is an infinite variety of ways in which the history of speciation and extinction in a group may have been non-random. For example, there may have been particular times of enhanced speciation or extinction, or rates of evolution may have changed in a regular or pulsed manner. Such patterns are best detected by directly calculating the number of speciations and extinctions per unit of time (Fig. 2.3.7.1a).

Within-tree variation in speciation and extinction rates

Speciation and extinction rates may also vary from one part of a tree to another (Fig. 2.3.7.1b). It is well established that different types of organisms have markedly different rates of taxonomic evolution (e.g. gastropods and mammals). Even within groups such as these there may be substantial variation in evolutionary rate due to inherited or ecological factors. If subgroups within a tree can be shown to have had significantly different rates of evolution, this may indicate important events such as the evolution of a 'key innovation' (see Section 2.3.1) and could even provide a degree of objective support for establishing higher taxa.

Tree balance is best defined as the extent to which internal nodes divide clades into groups of equal size, and can be measured in a variety of ways (see Mooers and Heard 1997). The within-tree variation depicted in Fig. 2.3.7.1(b) produces a markedly 'imbalanced' tree, which is the effect of a single node. Perhaps more interesting is the possibility that all the nodes of a tree combine to produce the imbalance. For example, if there is a bias for either ancestral or descendant taxa (in general) to become extinct or speciate, the resulting tree is likely to be exceptionally imbalanced. Two imbalanced shapes that have a long history in palaeontological speculation are shown in Fig. 2.3.7.2. In iterative evolution, species or higher taxa tend to be derived from a few 'ancestral stocks', each of which has a lower risk of extinction than its descendants. In step-series ('Stufenreihe') evolution the opposite is true. Examination of a variety of real trees (planktic foraminiferans, nannoplankton, and graptolites) demonstrates that ancestral taxa tend to branch much less frequently than their coexisting descendants and to become extinct first (Pearson 1998). This results in phylogenies that are considerably more imbalanced than could be expected by chance, in a way that conforms to the step-series model. The pattern may either be artificial or support Charles Darwin's original prediction from *On the origin of species by means of natural selection* that competitive interactions between taxa would shape the tree because 'at each period of growth all the growing twigs have tried to branch out on all sides, and to overtop and kill the surrounding twigs'.

Branch lengths

Another sort of general bias occurs where the speciation or extinction probability of a typical branch changes with its duration. For example, older (and thus potentially better established) taxa might be more resistant to extinction and more likely to speciate than they were soon after their time of origin. Alternatively, if evolution is progressive, older taxa might become 'out of date' and less able to compete. One way to test these possibilities is to use survival analysis to determine whether stratigraphic longevities conform to an exponential distribution (which they would if the probability of extinction was constant throughout their duration).

Palaeontological survival analysis is usually conducted on the total longevity of taxa from origination to extinction as determined from a range-chart. It is also possible, in principle, to analyse the lengths of internal and external branches (i.e. the durations between one branching point and another, or between branching and extinction). For example, analysis of a planktic foraminiferan phylogeny showed that internal branches were of unexpectedly short durations compared to external branches, implying a radiative pattern of evolution in which speciations occurred in quick succession as particular subgroups expanded (Pearson 1996) (Fig. 2.3.7.3).

Cladistic phylogenies

Temporal variation in speciation and extinction rates

It is very difficult to detect from a cladogram whether the historical rates of evolution of a group as a whole have changed in a systematic way (Fig. 2.3.7.1a). Certainly the rates themselves cannot be estimated without a measure of elapsed time. However, if the *relative* levels of speciation and extinction rates have changed with time, the number of taxa in a clade and the relationships between them would certainly be affected (see Mooers and Heard 1997).

Within-tree variation in speciation and extinction

It is now widely accepted among systematists that published cladograms tend to be more imbalanced than predicted by a random branching process of evolution (Fig. 2.3.7.4). This has led some authors to suggest that the various methods of tree construction impart imbalance even if none exists in the real phylogeny. Even though such biases do exist, most authors agree that studies of cladogram balance may be used in principle to study patterns of evolution (Mooers and Heard 1997).

It is possible to test the hypothesis that rates of evolution vary from one part of a tree to another (Fig. 2.3.7.1b) using cladograms. The most intuitive method is to calcu-

late the expected distribution of subclade sizes that would arise from a randomly branching model. For example, cladograms of 41 taxa would be split at their base into groupings of 40 and 1 taxa in only 5% of cases (Mooers and Heard 1997). This approach was adopted by Purvis *et al*. (1995) in their study of primate phylogeny; they were able to demonstrate that certain subgroups within the primates (such as Old World monkeys) have enjoyed unusually high rates of diversification compared to other groups.

Branch lengths and apomorphy distribution

Branch lengths on most cladograms (such as Fig. 2.3.7.4) simply reflect the branching order in the clade and have little intentional meaning. Alternatively, branch lengths can be made to signify inferred time or the genetic or morphological distance between taxa. There has been a substantial amount of interest in comparing molecular distances with divergence times, specifically to test the 'molecular clock' hypothesis that nucleotide substitutions occur at a stochastically constant rate (Fig. 2.3.7.5). Deviations from clock-like behaviour may be related to factors such as varying population size or generation time, and are thus of interest to the evolutionist.

A somewhat neglected aspect of cladogram shape is the distribution of apomorphies (characters) on the tree. Mindell *et al*. (1989) suggested that the hypothesis of punctuated equilibrium could be tested by considering the number of genetic substitutions acquired by the various taxa on a cladogram. Specifically, they argued that evolutionary lineages that have evolved through many splits would be likely to have had more substitutions in a period of time than lineages of the same duration with fewer splits (because evolution is predicted to have occurred predominantly during splitting events). They found support for this theory in their analysis of a lizard genus, although the particular phylogeny they used has subsequently been contested.

It is also fruitful to consider the question of apomorphy distribution in the context of cladogram symmetry. Both iterative and step-series processes (Fig. 2.3.7.2), for example, should produce imbalanced cladograms, but the former should result in a higher proportion of apomorphies on external (terminal) branches, whereas the latter should lead to their concentration on internal branches (Pearson 1999). Unfortunately, there are formidable problems associated with assessing apomorphy distribution on real trees because a variety of possible artefacts, which have yet to be fully assessed, might bias the distribution.

Conclusion

Although stratigraphic trees and cladograms differ in some profound ways, many of the most important questions of shape apply to both types of tree. Once a non-random pattern has been identified, the biggest challenge is to determine whether it is the result of some artificial bias or reflects a genuine evolutionary process. If the pattern is real, it will undoubtedly be of interest for understanding the evolutionary history of the group in question. If the same pattern is found repeatedly in many disparate groups, it is likely to be of general importance in understanding how evolution works.

References

Mindell, D.P., Sites, J.W. and Graur, D. (1989) Speciational evolution: a phylogenetic test with allozymes in *Sceloporus* (Reptilia). *Cladistics* **5**, 49–61.

Mooers, A.O. and Heard, S.B. (1997) Inferring evolutionary processes from phylogenetic tree shape. *Quarterly Review of Biology* **72**, 31–54.

Pearson, P.N. (1996) Cladogenetic, extinction and survivorship patterns from a lineage phylogeny: the Paleogene planktonic foraminifera. *Micropaleontology* **42**, 179–188.

Pearson, P.N. (1998) Speciation and extinction asymmetries in paleontological phylogenies: evidence for evolutionary progress? *Paleobiology* **24**, 305–335.

Pearson, P.N. (1999) Apomorphy distribution is an important aspect of cladogram symmetry. *Systematic Biology* **48**, 399–406.

Purvis, A., Nee, S. and Harvey, P.H. (1995) Macroevolutionary inferences from primate phylogeny. *Proceedings of the Royal Society of London B* **260**, 329–333.

2.3.8 Contingency

S.J. GOULD

Introduction

The subject of contingency embraces one of the deepest and grandest issues that we can fruitfully engage in science—the nature and status of history in comparison with the more conventional style of explanation by predictable and repeated occurrence under timeless and invariable laws of nature. The narrative sequences of history are, in no sense, incomprehensible or inaccessible to science, but historical explanation must differ from the standard experimental model if only because the subject matter embodies two properties seemingly contrary to basic criteria of 'the scientific method': (1) events that can occur but one time in all their detailed glory (and

where satisfactory explanation must encompass these details as well as any underlying generality); and (2) events that cannot—in principle, and not merely as a limitation of attainable human knowledge—be predicted from antecedent conditions, but only explained after their probabilistic occurrence.

Philosophers of science and history have long recognized this distinction between two basic styles of science—called the *nomothetic* vs. the *idiographic* (that is, repetition under laws vs. historically unique) in most philosophical writing, but named the *immanent* vs. the *configurational* by G.G. Simpson in an important article that urged the same distinction (Simpson 1963). If we define science in P.B. Medawar's terms as the 'art of the soluble'—that is, as the search for testable knowledge about the empirical world, both in factual character and in theoretical explanation—then both styles qualify as twin pillars of the broader enterprise. But the two styles differ in their basic working methodologies.

The more conventional nomothetic style encompasses repeatable phenomena that arise as consequences of the spatiotemporally invariant laws of nature—the classical movement of a perfectly spherical ball down a frictionless inclined plane, for example (where real balls and planes permit results 'close enough' to the unrealizable ideal). Nomothetic phenomena embody the great virtue of predictability. We can be fairly confident about the properties of Cambrian quartz before we find any, or even of a Jurassic rainbow (which we can never see in principle), because these relatively simple phenomena arise repeatedly under laws of physics and chemistry, and hold no historical uniqueness.

But most phenomena of life's history, the subject matter of palaeontology, fall into the idiographic category of historical items that arose for perfectly good and potentially understandable scientific reasons, but that did not have to occur as necessary (and therefore predictable) consequences of natural laws. Such items, rather, occur as contingent consequences of causal strings of unique historical events, each of which could have unfolded in a variety of plausible ways—but happened, empirically, to occur as they did. Such historical events (obviously) violate no laws of nature; moreover, knowledge of natural laws can help us to explain these events (the physics of impact provides important clues for understanding the effects of the bolide that triggered the K–T extinction). However, actual outcomes cannot be predicted from these laws, but rather arise as consequences of the complex and historically unique antecedent material conditions that produced these items in this particular run of history's 'tape'. Such idiographic events are therefore fully explainable after they occur (that is, they are *postdictable* in philosophical jargon). But idiographic events are not predictable before their unfolding because they arise as consequences of contingent strings of antecedent conditions at each step, and not as necessary results of nature's laws.

Contingency as good science

Professional historians, who treat such items as their stock in trade, refer to this style of idiographic causation as *contingency*. For example, the great American Civil War historian James McPherson (1988) argued that scientific explanation by contingency embodies two primary features. First, unpredictability of outcome in principle based on primary causation by particular antecedent conditions, rather than by natural law. Contingent explanation after the fact may be just as rigorous, and just as confident, as anything attainable in conventional nomothetic science, but predictability before the fact cannot be achieved as a principled consequence of nature's genuine complexity, not as a sign of human fallibility. McPherson writes (1988, p. 858): 'Most attempts to explain Southern defeat or Northern victory lack the dimension of contingency—the recognition that at numerous critical points during the war things might have gone altogether differently.'

Second, and methodologically, contingent explanations work best in the narrative mode—that is, by the documentation of actual history in temporal order (since primary causes of the outcome lie in particular events of the sequence, and not in timeless laws that regulate all outcomes to be sure, but in too broad a manner to encompass the particulars sought in historical explanation).

This framework strikes most scientists as clear, fair, and uncontroversial in itself. Difficulties tend to arise for reasons of human psychology and sociology when, for a variety of reasons largely contingent within the flow of western history, the idiographic style becomes denigrated as less than, or only imperfectly, scientific, and when a consequent ordering of status raises nomothetic science either to pre-eminent prestige, or even to presumptive exclusivity. Only in one sense might we fairly grant a form of practical preference to nomothetic explanation. Since nomothetic items are predictable under natural law, we need not know the detailed sequence of antecedent conditions to render an explanation. Cambrian quartz owes its internal organization to the temporally invariant behaviour of oxygen and silicon ions. But explanation of idiographic items does require knowledge of particular antecedent conditions—and such evidence, given the inevitable imperfection of historical records (particularly the geological record), often does not exist. Explanations for eye rows in the Devonian trilobite *Phacops rana* depend partly upon nomothetic principles of optics, but also upon idiographic sequences of particular ancestral forms and environments—information that may not be preserved in sufficient detail in our spotty historical archives.

Most conventional reasons for preferring the nomothetic mode only record our psychological hopes and preferences (our general desire for the reassurance of predictability in an uncertain world, or our more particular need to view our own, and very recent, evolution as a necessary outcome rather than a contingent accident of good fortune)—and we must struggle against such dictation of science by contingent human predilection. Idiographic science holds just as much fascination, just as much challenge and excitement, just as much promise for insight and rigorous explanation, as anything achieved by particle physics. Moreover, idiographic methods are both appropriate and necessary for understanding the history of life—so we cannot avoid contingency by wishing for a predictable pageant from Precambrian bacteria to the full flower of modern diversity.

Contingency as both conventional and radical

As perhaps the oddest attribute of this subject within palaeobiology, contingency ranks both as the oldest and least controversial aspect of our discipline and, in another guise, as a source of deep and considerable theoretical struggle in our times. The basic concept of contingency lies at the heart of Darwin's revolution, and represents a central and explicit insight within his formulation of natural selection. Pre-Darwinian evolutionary systems advocated a basic distinction between an overarching and pre-eminent nomothetic cause of predictable directionality within the history of life, and a secondary, confusing idiographic cause of local peculiarity (giraffe's necks and eyeless moles). Lamarck, for example, contrasted a primary 'cause which tends incessantly to complicate organization'—a nomothetic property of organismic physics that drives evolution up a predetermined ladder of progress—with a secondary and idiographic 'influence of circumstances' which causes particular lineages to deviate orthogonally into lateral branches of local adaptation by inheritance of acquired characters (moles losing eyes by disuse, and giraffes stretching necks to reach acacia leaves).

Darwin, in a brilliant argument, denied that the nomothetic drive existed as a causal principle at all, and then sought to render all of life's history as an extrapolated consequence (through the immensity of geological time) of idiographic circumstances—the principle of natural selection, working only (and incessantly) at the level of local adaptation to immediate environments. (Macroevolutionary patterns include predictable aspects, but their causal root, in Darwinian theory, lies in natural selection on organisms of local populations in surrounding environments.)

Thus, Darwinian evolutionists have always recognized that their basic theory of evolutionary change (natural selection) must underpredict the actual pattern of life's history, and that a resolution of the temporal pageant must be achieved by historical methods, primarily by documentation of the fossil record. In this sense, Darwinism has always granted a large and independent domain to palaeontology.

But, in another sense that has made contingency a controversial issue within modern palaeontology, conventional Darwinism has also held palaeontology on a leash by the following argument:

We grant you the documentation of actual pattern, for our basic theory cannot predict these details of contingent history. But we hold all the theory necessary for specifying the basic directions and overarching generalities of life's history—so you get the details while we retain the reasons for the generalities.

The controversial character of modern views about contingency may be summarized in the counter claim that many of the broad generalities fall into the domain of contingent explanation as well—and that the evolutionary sciences need historical methods to explain not only the particular items of the pageant, but also the generalities of the pattern.

Of course, no one denies the importance of nomothetic pattern in life's history. Many arguments about adaptation must invoke the biomechanics of good design, while many properties of ecosystems must record the basic physics of energy flow, and must therefore arise repeatedly and predictably (greater biomass in prey than in predators, for example). But many aspects of even the broadest patterning in life's history—why and when do multicellular organisms arise, why and when do mammals eventually inherit the environments of large terrestrial vertebrates from dinosaurs—fall largely (or at least importantly) into the domain of contingent explanation. Moreover, even the most nomothetic of predictable details (common aerodynamic properties of convergent wings in bats, birds, and pterosaurs, for example) can only arise from the contingent substrates of particular antecedent structures (the forelimbs of terrestrial vertebrates as historically evolved from fins in a small and marginal lineage of ancestral fishes).

Conclusion

Three examples illustrate how intense palaeontological discussion has focused on claims for contingent explanation of important patterns that had previously been granted to the domain of nomothetics.

1 *The emergence and stabilization of modern animal phyla from the results of the Cambrian explosion*. I have argued elsewhere (Gould 1989) that the reinterpretation of the Burgess Shale fauna by H.B. Whittington and colleagues had revealed a pattern of maximal disparity after the Cambrian explosion (more basic anatomical designs

even than in modern seas, but with far fewer species), followed by contingent and unpredictable extinction of most designs (death for causal reasons of immediate circumstances, but bearing no relationship to such putatively predictable larger scale factors as increasing complexity, flexibility, or general excellence of biomechanical design). In this sense, if we could 'wind back life's tape' to the Burgess fauna, making no change except a redistribution of 'lottery tickets' for contingent survival from the initial 'overshoot' of designs, the history of life would unfold in an entirely different, but equally explainable way—with low probability for the evolution of vertebrates, virtually no chance of human origin, and little expectation of any conscious species at all. Conway Morris (1998) has attempted to refute this argument for contingency by stressing the importance of convergence as a nomothetic phenomenon granting reasonable predictability to the broad features of life's history (see also Section 5.1.3).

2 *The replacement of dinosaurs by mammals.* Traditional views of non-catastrophic mass extinction assumed a basically predictable death of dinosaurs during a prolonged period of climatic stress that enhanced the usual Darwinian struggle and led to the eventual triumph of mammals for reasons of competitive advantage (in conditions of such stress, not necessarily in direct 'combat' with much larger dinosaurs), based on conventional accounts of general mammalian superiority. The catastrophic scenario of bolide impact suggests a radical revision, citing fortuitous removal of successful dinosaurs with serendipitous survival of mammals, based not on superior designs leading to eventual and predictable domination in any circumstance, but rather on contingent good fortune of features that could weather the global storm—traits (such as small body size) that may record previous 'failures' (inability to supplant dinosaurs in Darwinian competition for habitats of large-bodied vertebrates in normal times) rather than predictable competitive virtues. In this crucial sense, humans now exist by contingency. No bolide, no dinosaur extinction—and mammals might still be living as small creatures in the nooks and crannies of a dinosaur's world.

3 *The 'out of Africa' vs. 'multiregional' theories for the origin of* Homo sapiens. This intense debate (see Section 1.5.5) basically represents an episode in the larger discourse between contingency and predictability in the history of life. The multiregional view—holding that *Homo sapiens* evolved in parallel from three basically separate *H. erectus* stocks (with limited gene flow) in Africa, Europe, and Asia—views 'sapienization' (as the process has been called) as a predictable Darwinian result of the general superiority of human mental traits (for how else could the same set of features arise in three parallel lines?). The 'out of Africa' view supports the contingent scenario that even the most awesome and successful adaptations (in retrospect, though perhaps we should not so flatter ourselves) arise as immediate and unpredictable features in historically unique local populations—in this case the origin of *H. sapiens* as a single contingent branch from African populations of *H. erectus*. The growing evidence, both genetic and palaeontological, for 'out of Africa' can only reinforce the importance of contingency, and urge us all to set aside our conventional preferences (based on factors ranging from traditional arguments for intrinsic human importance to the differential status of nomothetic vs. idiographic science), and to grant equal weight and prestige to the yin and yang of predictable and contingent factors in the history of life.

References

Conway Morris, S. (1998) *The crucible of creation*. Oxford University Press, Oxford.

Gould, S.J. (1989) *Wonderful life: the Burgess Shale and the nature of history*. W.W. Norton, New York.

McPherson, J. (1988) *The battle cry of freedom*. Oxford University Press, Oxford.

Simpson, G.G. (1963) Historical science. In: C.C. Albritton, ed. *The fabric of geology*, pp. 24–48. W.H. Freeman, San Francisco.

2.3.9 Selectivity during Extinctions

M.L. McKINNEY

Introduction

Extinction is very rarely random at any spatial or temporal scale. At large (regional or global) scales, it has probably never been random. This is because of the many differences among species in their genetic, physiological, population, and other traits which can influence species responses to change. Selectivity refers to this non-random property of most extinctions, including all mass extinctions.

Extinction selectivity is an old idea. Lamarck speculated that marine organisms were less prone to extinction than terrestrial organisms because they were more buffered against environmental change. In his *Principles of geology*, Charles Lyell discussed at length the selective nature of extinction. Darwin devoted considerable attention to dominant species that resisted extinction because they were both more abundant locally and had a very wide geographical range. Another early theme promoted by G.G. Simpson, and still very common in dis-

cussions of species risk in the conservation literature, is that broadly adapted 'generalist' species persist longer in the geological record. The onset of the modern extinction crisis has produced a rapid growth of publications, especially in ecology, about proneness to extinction. In palaeontology, selectivity has been most often debated in the context of mass extinctions, although group differences in extinction-proneness exist at all scales, as shown by taxonomic differences in background extinction rates.

Types of extinction selectivity

Many types of selectivity have been discussed in palaeontology. This is to be expected, given: (1) the many kinds of environmental disturbances that have occurred; and (2) the evolution of biotic traits so that extinction-proneness is not a static property among taxa. Extinction selectivity is the product of the complex interplay between these two factors, the extrinsic environmental disturbances that occur and the intrinsic biotic properties of species that determine their response to the disturbance. The complex nature of this extrinsic–intrinsic interplay requires that extinction selectivity be analysed as a probabilistic (statistical) pattern of sorting among groups of species rather than a deterministic phenomenon (Brown 1995).

Three of the most basic types of extinction selectivity are trait, taxonomic, and geographical selectivity. Trait selectivity occurs when biotic traits, such as trophic level, body size, or abundance, directly influence extinction-proneness (see Jablonski 1995, 1996). Taxonomic selectivity refers to different species extinction rates among higher taxa, usually at mass extinction events. An example is the higher rate of species extinction among dinosaurs compared with mammals during the K–T mass extinction (Archibald 1996). Geographical selectivity occurs when extinction rates are relatively higher in some regions than others.

It is often useful to compare selectivity patterns among different periods of time. This can help to identify physical causes of extinction, and it provides important data on macroevolutionary dynamics and related clade-level properties. Three basic categories of selectivity have been proposed in the context of geological time: fair game, wanton selectivity, and field of bullets (Raup 1991). Fair game selectivity occurs when the traits and taxonomic membership that promote survival during a mass extinction event are the same as those that promoted survival during 'normal' (background) geological time. Wanton selectivity, on the other hand, occurs when they differ. Field of bullets selectivity occurs when species survival is random with respect to the traits or taxonomic membership.

Trait selectivity

Extinction selectivity is determined by the specific kind of environmental changes that occur and the composition of the biotas that are subjected to them. Because mass extinctions have had a variety of different physical causes, they have often varied in their patterns of taxonomic and ecological selectivity (Erwin 1993; Archibald 1996; McGhee 1996). The emerging evidence implies that both fair game and wanton selectivity were common during most (if not all) mass extinctions because background patterns of selectivity were not entirely disrupted (Erwin 1993; Archibald 1996; Jablonski 1996; McGhee 1996). This implies that some traits that reduce survival during normal 'ecological' time also do so during times of catastrophic change. If true, this would explain why the traits reported to promote extinction in the ecological literature are the same as those commonly implicated in the palaeontological literature (Table 2.3.9.1). Three of the most important and widely cited traits in both cases are specialization, large body size, and low abundance.

Many extinction-promoting traits are associated with specialization, suggesting that these traits may covary. Such covariation is supported by the evidence that a species broadly adapted in one parameter, such as temperature tolerance, is also broadly adapted in other parameters, such as diet, and tends to be more locally abundant and widespread (Brown 1995). Conversely, narrowly adapted 'specialist' species can tolerate less change in a number of niche parameters and tend to be less locally abundant and geographically widespread. Specialized species may thus be prone to multiple jeopardies produced by a synergistic combination of fewer individuals with narrower tolerances to change (Brown 1995). There is strong evidence for the preferential survival of generalist species during many mass extinctions (see Erwin 1998). Examples include a high proportion of omnivores and eurytopes among surviving species.

Large body size is another one of the most commonly cited traits promoting extinction risk in both ecology and palaeontology. However, it is not a universal predictor of extinction. There are examples of positive, negative, and no relationship between body size and extinction risk, probably because body size influences abundance and population fluctuations in complex ways that vary among taxa. For molluscs in the Late Cretaceous (K–T) mass extinction, body size was not a factor in survivorship (Jablonski 1995, 1996). In contrast, small body size seems to have promoted survival of land vertebrates (Archibald 1996) and sea urchins (Smith and Jeffery 1998) during the K–T mass extinction.

Rarity is another widely cited trait promoting extinction (Table 2.3.9.1). Two common measures of rarity are localized geographical range and low density. These two

Table 2.3.9.1 Biological traits cited in the ecological and palaeontological literature as increasing extinction risk. Symbols: ++, many citations identified; +, at least one citation identified; –, none identified so far. Sources listed by McKinney (1997).

Traits	Modern extinctions	Fossil extinctions
Specialization		
Stenothermy	++	++
Specialized diet	++	++
High trophic level	++	++
Symbiotic	++	+
Large body size	++	++
Low fecundity	++	+
Long-lived	++	+
Slow growth/development	++	+
Complex morphology	+	++
Complex behaviour	+	+
Less mobility	++	–
Migratory	++	–
Aquatic biotas		
Planktic	+	++
Epifaunal	+	++
Filter-feeder	+	++
Coarse filter-feeder	–	+
Non-benthic larvae	+	+
Non-brooding larvae	–	+
Small colonies (corals)	–	+
Abundance		
Low mean abundance (*K*)	++	++
Localized range	++	++
Low density	++	++
High variation	++	+
Slow increase (*r*)	++	–
Seasonal aggregations	++	–
Low genetic variation	++	–

types of rarity are not independent. There is evidence at many scales that geographical range and local abundance are generally correlated, so that rare species tend to have both narrow geographical ranges and sparse population densities (Brown 1995). Other important traits related to abundance that promote extinction are high abundance variation and low rate of intrinsic growth (Table 2.3.9.1).

Taxonomic selectivity

Environmental disturbances that produce trait selectivity may also produce patterns of taxonomic selectivity (Fig. 2.3.9.1). Such highly selective taxonomic extinction can reduce biodiversity much more rapidly than random extinction (McKinney 1997). Taxonomic selectivity often occurs because body size, abundance, niche-breadth,

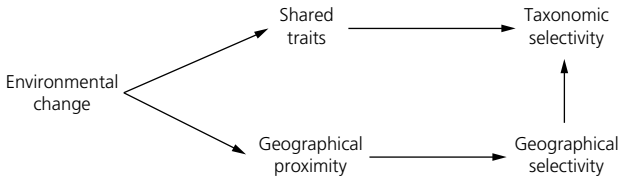

Fig. 2.3.9.1 Extinction-biasing traits cause taxonomic selectivity because they are non-randomly distributed among higher taxa. Non-random geographical proximity of related species is another source of taxonomic selectivity because of regional variation in the intensity of environmental disturbances.

and many other extinction-biasing traits (Table 2.3.9.1) have a significant genetic (heritable) component. Therefore, evolutionary branching can concentrate extinction-biasing traits into certain taxa at many taxonomic levels (Gaston and Blackburn 1997). Evidence for clustering of extinction-biasing traits includes the non-random taxonomic clustering of rare species in some North American bird families and plant families, widespread species in some genera of living echinoids and fossil molluscs, and large-bodied birds in some higher taxa (McKinney 1997). The concentration of rare species, for example, in certain higher taxa would thus tend to promote high extinction rates in those taxa, given that rarity is a major feature promoting extinction (Brown 1995).

There is also a large palaeontological literature documenting differences in extinction rates among many taxonomic levels (from genera through phyla) during both background geological time and mass extinction events (Jablonski 1995, 1996). Well-known examples include the shorter average species duration of ammonites and mammals compared to bivalves and other slowly evolving taxa. It is difficult to relate differences in extinction rates among such higher taxa to specific biological variables. In addition, the coarse temporal and taxonomic scales of these data are susceptible to many artefactual biases that may produce biologically misleading patterns. One of the most problematic is differential preservation among taxa caused by taxonomic biases in mineralogy, life habits, and abundance. These could produce artefactual taxonomic extinction patterns that are very similar to those observed. Nevertheless, the palaeontological literature is rich with suggestions about the causes of different background extinction rates among higher taxa. Such suggestions have included the greater environmental volatility of terrestrial habitats (mammals) compared to marine habitats (bivalves), and the higher risk of extinction for morphologically complex taxa (mammals, ammonites) compared to simpler taxa (bivalves).

More progress has been made in dissecting the differential responses of higher taxa at specific mass extinction

events. Artefactual patterns are reduced by gathering high-quality data on a specific interval and by analysing at a finer taxonomic resolution where more clear-cut biological causes of selectivity can be discerned. Examples include the often striking patterns of taxonomic extinction selectivity recorded at the end-Devonian (McGhee 1996), end-Permian (Erwin 1993), and K–T (Archibald 1996) mass extinctions. The advantages of fine-scale studies are illustrated by an analysis of differential extinction among echinoid orders at the K–T event (Smith and Jeffery 1998). The selective taxonomic patterns can be attributed to a number of trait correlates (trait selectivity) such as adult feeding strategy and body size. Such a study also provides many important data on causal physical mechanisms of catastrophes, in this case the nature, location, and duration of the global disturbances behind the K–T extinctions (and aftermath).

Geographical selectivity

Geographical extinction selectivity occurs because most catastrophic events, as well as more frequent background disturbances, do not influence all regions with equal magnitude. Both background and mass extinction rates vary among geographical biotas (Flessa and Jablonski 1996). Geographical selectivity may also cause taxonomic selectivity (Fig. 2.3.9.1) because related species tend to be found in geographical proximity (Gaston and Blackburn 1997).

Three basic categories of habitats are often contrasted: terrestrial–marine, terrestrial–freshwater, and tropical–non-tropical, where the first of each pair is usually considered to contain more extinction-prone species. The terrestrial–marine pair illustrates a relationship between taxonomic and habitat vulnerability. Higher taxa in the marine environment tend to have lower extinction rates than mainly terrestrial taxa (McKinney 1997). This appears to be true for the current extinction crisis and for past geological background extinctions. In addition to having more widespread species, the marine environment may buffer species from rapid physical changes. Within the marine realm, deep-water species seem to have preferentially survived the Late Devonian and Late Permian mass extinctions.

The global cooling that caused the Late Devonian extinction, and the sea-level fluctuations and meteorite impact that caused the late Mesozoic extinction, are both characterized by non-random survival of freshwater biota. This has been attributed to the ability of freshwater biota in the Late Devonian to better tolerate seasonal and other physical fluctuations (McGhee 1996). The survival of the freshwater biota following the Late Cretaceous meteorite impact has been related to a detritus-based food web that buffered the effects (Archibald 1996).

Marine tropical species are geologically younger and, on average, have higher extinction rates than non-tropical species (Flessa and Jablonski 1996). This could be due to narrower ecological tolerances and/or narrower geographical ranges of tropical species. In past mass extinctions, tropical taxa have been preferentially eliminated. Examples include the Late Devonian (McGhee 1996), Late Permian (Erwin 1993), and Late Cretaceous (Archibald 1996). Tropical losses often include high-diversity tropical reefs and their associated biotas.

Conclusions

Evidence from background and mass extinctions indicates that, of the three selectivity categories (Raup 1991), both fair game and wanton selectivity are common, while field of bullets (random extinction) is never found (Erwin 1993; Archibald 1996; McGhee 1996; McKinney 1997). Such accumulating evidence will be a key to resolving the long-standing, often philosophical, debate over whether evolution is a fundamentally random process. Given the wide variety of non-random traits and geographical distributions among taxa, it is hardly surprising that non-random extinction is the rule. Nor is it surprising, for the same reasons, that mass extinctions show a combination of fair game and wanton selectivity patterns. Because so many traits vary non-randomly among taxa, any major catastrophe will almost certainly selectively favour some traits that have favoured survival in the past, as well as some traits that did not promote extinction.

The common occurrence of trait, taxonomic, and geographical extinction selectivity has important implications for the rate at which diversity is lost during large environmental disturbances. All three types of selectivity may accelerate the loss of biological diversity. Selective removal of certain traits or higher taxa, for example, can potentially eliminate diversity much faster than if traits or taxa are eliminated at random (McKinney 1997). In addition to accelerating the loss of net global diversity, extinction selectivity can also increase the homogenization of the remaining diversity on Earth. Homogenization refers to the loss of spatial diversity when specialized endemic species are replaced by the same few widespread generalist species, a process that occurs during many mass extinctions (Erwin 1998). The concentration of successful (i.e. generalist) species in some taxa and unsuccessful species in other taxa could significantly promote homogenization of the biosphere because surviving species would tend to be more closely related than extinct species.

References

Archibald, J.D. (1996) *Dinosaur extinction and the end of an Era*. Columbia University Press, New York.

Brown, J.H. (1995) *Macroecology*. University of Chicago Press, Chicago.
Erwin, D.H. (1993) *The Great Paleozoic Crisis*. Columbia University Press, New York.
Erwin, D.H. (1998) The end and the beginning: recoveries from mass extinctions. *Trends in Ecology and Evolution* **13**, 344–349.
Flessa, K.W. and Jablonski, D. (1996) The geography of evolutionary turnover: global analysis of extant bivalves. In: D. Jablonski, D.H. Erwin and J.H. Lipps, eds. *Evolutionary paleobiology*, pp. 376–397. University of Chicago Press, Chicago.
Gaston, K.J. and Blackburn, T.M. (1997) Evolutionary age and risk of extinction in the global avifauna. *Evolutionary Ecology* **11**, 557–565.
Jablonski, D. (1995) Extinctions in the fossil record. In: J.H. Lawton and R.M. May, eds. *Extinction rates*, pp. 25–44. Oxford University Press, Oxford.
Jablonski, D. (1996) Mass extinctions: persistent problems and new directions. *Geological Society of America Special Paper* **307**, 1–9.
McGhee, G.R. (1996) *The Late Devonian mass extinction*. Columbia University Press, New York.
McKinney, M.L. (1997) Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annual Review of Ecology and Systematics* **28**, 495–516.
Raup, D.M. (1991) *Extinction: bad genes or bad luck?* Norton, New York.
Smith, A.B. and Jeffery, C.H. (1998) Selectivity of extinction among sea urchins at the end of the Cretaceous period. *Nature* **392**, 69–71.

2.3.10 Biotic Recovery from Mass Extinctions

D.J. BOTTJER

Introduction

Much work has been directed towards understanding the causes of mass extinctions, but comparatively little has addressed the patterns and processes of recovery from these biotic crises. The work that has been done on recoveries typically has been constrained by the time resolution available and the taxonomic expertise of the palaeontologist. Yet the subject of recovery from mass extinctions is widely recognized as one that should be high on the agenda of palaeobiological research. Understanding how the Earth's biota has recovered from mass extinctions is significant because not only is it necessary to understand these processes to appreciate life's bumpy progression through the Phanerozoic, but it also helps us to appreciate the fragility of the Earth's ecosystems, which are under constant assault in the modern world.

Perhaps the best illustration of the importance of recovery intervals in the history of life is provided through work done to define and analyse 'Ecological Evolutionary Units'. These 'EEUs' are distinctive long intervals of geological time in the Phanerozoic history of life during which benthic palaeocommunities are composed of a static array of genera (Boucot 1983; Sheehan 1996) (see Section 4.2.1). Originally the marine Phanerozoic fossil record was subdivided into 12 EEUs (Boucot 1983). However, later work has determined that the short intervals following several of the mass extinctions are not EEUs, but represent recovery intervals 'characterized by instability, recurrent replacements and reorganizations of communities' (Sheehan 1996, p. 23). These 'intervals of reorganization' (Sheehan 1996), observable on a Phanerozoic time scale, range from 3 to 8 myr long, while EEUs represent intervals of ecological stability ranging from 30 to 140 myr long.

Nine EEUs and five recovery intervals are recognized in the Phanerozoic, with each of the latter occurring after one of the 'Big Five' mass extinctions (end-Ordovician, end-Devonian, end-Permian, end-Triassic, and end-Cretaceous). Observable recoveries also occurred after mass extinctions other than the 'Big Five' (e.g. Kauffman and Harries *in* Hart 1996), but their ecological structure is not sufficiently different to separate them from the EEU in which they occur. Nevertheless, much has been learned about recovery processes from these smaller mass extinctions, particularly in the Cretaceous at the Cenomanian–Turonian boundary (e.g. Kauffman and Harries *in* Hart 1996; see also other chapters in Hart 1996).

In reconstructing recovery processes for EEU recovery intervals, as well as after other smaller mass extinctions, analysis of palaeoenvironments and palaeoecology can pose difficulties because these times of changing ecospace utilization may not show similar ecological structures to those found in modern environments. Thus when studying biotic recovery from mass extinctions, a non-actualistic analytical approach is commonly warranted (Bottjer 1998).

Each recovery from a mass extinction appears to have a unique signature, depending upon the influence of several factors that determine the nature of biotic recovery: (1) the taxonomic effect of the mass extinction, as measured by taxonomic loss (e.g. Hallam and Wignall 1997), as well as the types of organisms that remain (and their diversity); (2) the effect of the mass extinction upon ecological structure, best measured in an overall sense by using the approach of 'comparative evolutionary palaeoecology' (Bottjer *et al. in* Hart 1996), and exemplified by the system of palaeoecological levels (see Section 4.2.1) (a finer scale of analysis is, however, also possible); (3) whether the environmental stress(es) that caused the mass extinction was confined to the mass extinction interval, or continued

at some reduced level, thus inhibiting the recovery; and (4) the location and size of geographical and environmental refugia.

Studies of recovery intervals have shown that a temporal structure can be discerned within them, characterized by differing biotic features. This temporal structure has been resolved to different degrees, depending upon whether a theoretical approach was taken (e.g. Harries *et al*. *in* Hart 1996), or whether a particular mass extinction (e.g. end-Permian, end-Cretaceous) was being studied. In defining the internal structure of a recovery interval, the usual approach (followed herein) has involved the analysis of taxonomic diversity data. As more is learned, a variety of palaeoecological data will also be incorporated into definitions of recovery interval temporal structure. The following temporal structure combines features from several studies (e.g. Hallam and Wignall 1997): (1) *mass extinction*—taxonomic diversity drops relatively rapidly, as extinction rate is greater than origination rate; (2) *survival* or *lag*—taxonomic diversity 'levels out', as extinction rate approximately equals origination rate; (3) *rebound*—taxonomic diversity begins to increase again, with the reappearance of Lazarus taxa, and as origination rate becomes greater than extinction rate; and (4) *expansion*—taxonomic diversity increases at an even greater rate due to a further increase in origination rate relative to extinction rate.

The recovery interval is defined as lasting from the end of the mass extinction until after the expansion has commenced. Not all recoveries after mass extinctions show this temporal structure, and segments may be absent. Different temporal structures can be found in recoveries depending upon temporal differences (e.g. the rate at which a recovery proceeded, or the time resolution at which the study was done). Different temporal structures may also be documented in different ecosystems after the same mass extinction (e.g. planktic vs. benthic; marine vs. terrestrial). Variations in temporal structure of a recovery interval may also have a geographical component. Thus, depending upon the focus of a study, different temporal structures for the recovery interval could be defined for the same mass extinction.

Two major data collection and analysis methodologies have been applied to the study of recoveries, termed here the 'taxonomic' and 'palaeoecological' approaches. As modern mass extinction studies were pioneered by a taxonomic approach, taxonomic analyses of recoveries have been the most prevalent (e.g. Hart 1996; Hallam and Wignall 1997).

Taxonomic approaches

Taxonomic data used in the reconstruction of biotic recoveries from mass extinctions rely on the presence or absence of taxa with particular phylogenetic/evolutionary features within a temporal or geographical framework. These data are typically retrieved from literature or museum collections. Much data originally collected for biostratigraphic purposes are particularly suitable for these types of analysis. In developing a vocabulary for more precise communication on biotic recoveries, several different types of taxa have been defined, sometimes with novel yet informative names.

1 *Lazarus taxa* vanish from the stratigraphic record during a mass extinction, are not present during part or most of the recovery, and then reappear in the record (Fig. 2.3.10.1) (Jablonski 1986). The number of Lazarus taxa has been interpreted to indicate the importance of refugia during a mass extinction (e.g. Hallam and Wignall 1997), or possibly the number of species that did not go extinct but whose populations reached such low levels during the recovery that they produced only rare fossils that are unlikely to be collected (Hallam and Wignall 1997).

2 *Elvis taxa* show the same temporal pattern as Lazarus taxa, but are only convergent with, rather than taxonomically the same as, morphologically similar pre-extinction taxa (e.g. Hallam and Wignall 1997).

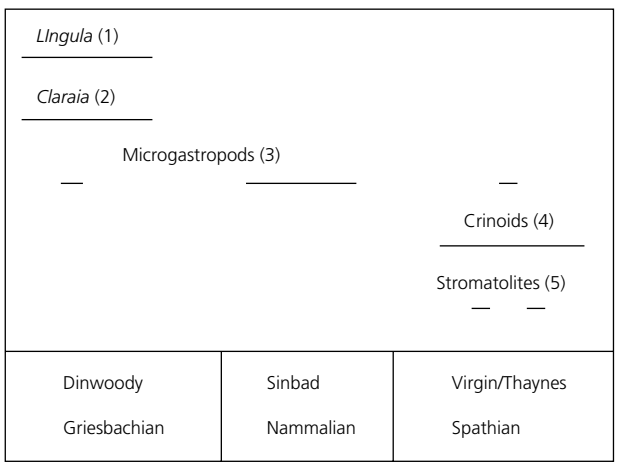

Fig. 2.3.10.1 Stratigraphic distribution of selected Early Triassic biotic recovery taxa, as well as stromatolites (range lines shown below each label) in strata deposited in neritic environments in the western USA, including: (1) a disaster taxon; (2) a progenitor taxon; (3) opportunists; (4) a Lazarus taxon; and (5) a disaster form. Data from the Griesbachian age Dinwoody Formation, the Nammalian age Sinbad Limestone Member of the Moenkopi Formation, the Spathian age Virgin Limestone Member of the Moenkopi Formation, and the Spathian age Thaynes Formation (primarily from Schubert and Bottjer 1992, 1995).

3 *Holdover taxa* belong to a higher taxon that experienced a significant level of loss in the mass extinction. Such taxa survive into the recovery interval, only to become extinct in the survival or lag phase (e.g. Hallam and Wignall 1997).
4 *Bloom taxa* experience an evolutionary burst during the recovery interval, and then subsequently decline (Hansen 1988).
5 *Progenitor taxa* first evolve during the mass extinction interval and survive to 'seed' the evolution of dominant groups during the recovery interval (Fig. 2.3.10.1) (Kauffman and Harries *in* Hart 1996).

Palaeoecological approaches

Palaeoecological data that are used for the reconstruction of biotic recoveries after mass extinctions include palaeocommunity and biofabric information as well as taxonomic data with an ecological component. Such data are not easily extracted from literature or museum collections and generally require new field studies. Important concepts include the following:
1 *Opportunists* (Fig. 2.3.10.1) are taxa that undergo a dramatic increase in abundance during the recovery interval (Hallam and Wignall 1997), typically due to relaxation of competition. Opportunists include *disaster taxa*, which are long-ranging taxa that become unusually abundant during the recovery interval (e.g. Hallam and Wignall 1997). This definition has been extended to include some microbial structures, and stromatolites found in Lower Triassic strata have been termed 'disaster forms' (Schubert and Bottjer 1992).
2 *Palaeocommunity structure* comprises data on community properties such as diversity, biogeographical distribution, species richness, number of 'Bambachian megaguilds' (adaptive strategies defined by life position and general feeding type; see also Section 4.2.1), and tiering (see also Section 4.1.4) (e.g. Bottjer *et al. in* Hart 1996).
3 *Biofabrics* are those sedimentary structures that are biologically mediated, and hence contain distinct biological information. Biofabrics include microbial structures as well as shell beds, trace fossils, and ichnofabric (e.g. Bottjer *et al. in* Hart 1996).
4 *Comparative evolutionary palaeoecology* provides a framework that allows palaeoecological data from before and after the mass extinction to be compared to that of the recovery interval (Bottjer *et al. in* Hart 1996). *Palaeoecological levels* (see Section 4.2.1) is a methodology of comparative evolutionary palaeoecology that provides a means to scale or rank palaeoecological change during major events in life's history, such as the ecological changes due to mass extinctions that occur in recovery intervals. The system of palaeoecological levels incorporates data from several of the other palaeoecological approaches listed above to allow evaluation of ecological change at four levels (first-level changes are of the greatest magnitude and represent the advent or loss of an ecosystem; second-level changes occur within an established ecosystem and represent major structural changes at the largest ecological scale; third-level changes include community-scale shifts within an established ecological structure; fourth-level changes are similar in magnitude to most minor ecological changes; see also Section 4.2.1).

Recovery from the end-Permian mass extinction

The end-Permian mass extinction was the largest biotic crisis of the Phanerozoic, when possibly as many as 90% of species became extinct (see Section 2.4.4) (Hallam and Wignall 1997). The magnitude of the mass extinction, and the resulting long recovery interval (7–10 myr), makes the recovery of benthic macroinvertebrates from this particular crisis more amenable to analysis than most. The large biotic effects and long time intervals help to counter some of the distortions of the fossil and stratigraphic record that are normally present. A variety of mechanisms have been implicated in the end-Permian mass extinction, including marine anoxia, eruption of the Siberian traps, and hypercapnia (CO_2 poisoning), and debate continues on whether the crisis represents one event or two in close succession (see Section 2.4.4) (Hallam and Wignall 1997). Whatever the cause, end-Permian environmental conditions wreaked such havoc on the Earth's biota that the Early Triassic has been viewed as the most profound 'dead zone' in the Phanerozoic fossil record, representing an unusually long recovery interval (e.g. Hallam and Wignall 1997). Debate on why recovery took so long has centred on three possibilities: (1) the mass extinction was so extensive that an unusually long period of time was involved in the recovery; (2) environmental stress related to the causes of the mass extinction continued to occur through most of the Early Triassic; and (3) preservation and sampling bias has skewed our perception of the fossil record (e.g. Schubert and Bottjer 1995; Erwin and Pan *in* Hart 1996). Although several biostratigraphic schemes have been utilized for the Early Triassic (e.g. Hallam and Wignall 1997), this interval is commonly divided into the Griesbachian (oldest), Nammalian, and Spathian stages (Fig. 2.3.10.1), which span a total of approximately 7–10 myr.

The pattern of gastropod occurrence from the Permian into the Triassic shows a variety of taxa that are absent from all or part of the Early Triassic fossil record; this was the first example to be recognized of what was later defined as the Lazarus effect (e.g. Jablonski 1986; Erwin and Pan *in* Hart 1996; Hallam and Wignall 1997). Crinoid

echinoderms are also absent from the early part of the Early Triassic fossil record (Fig. 2.3.10.1). If the Lazarus effect can be extended to the class level, then the Crinoidea is also a Lazarus taxon, with the youngest Permian crinoid in this sequence an inadunate, and the oldest Triassic crinoid an articulate. The Permian/Triassic mass extinction is thought to have caused the extinction of all but one genus of crinoids (e.g. Schubert and Bottjer 1995).

The Griesbachian commonly contains abundant specimens of the bivalve *Claraia* (Fig. 2.3.10.1), which first evolved in the latest Permian and then underwent an explosive evolutionary radiation from the Griesbachian into the Nammalian, thus giving it the characteristics of a progenitor taxon (Hallam and Wignall 1997). Many Lower Triassic intervals also contain beds composed almost entirely of tiny adult gastropods (Fig. 2.3.10.1); these microgastropods acted as opportunists in Early Triassic seas (see Section 2.4.4) (Schubert and Bottjer 1995; Hallam and Wignall 1997). Subtidal marine stromatolites are found in Lower Triassic carbonate facies at a variety of localities (e.g. Fig. 2.3.10.1), representing deposition marginal to the global Panthalassic Ocean and the Palaeo-Tethys (e.g. Schubert and Bottjer 1992; Bottjer *et al. in* Hart 1996), and these have been termed 'disaster forms'. In the Griesbachian the inarticulate brachiopod *Lingula* is perhaps as abundant worldwide as it is in any Phanerozoic strata (e.g. Fig. 2.3.10.1) (Schubert and Bottjer 1995; Hallam and Wignall 1997), and this long-ranging genus similarly has all the classic features of a disaster taxon.

Other palaeoecological effects of this mass extinction have long been known, including the presence of widespread cosmopolitanism among Early Triassic taxa (e.g. Hallam and Wignall 1997). Early Triassic palaeocommunities are dominated overwhelmingly by bivalves (e.g. Schubert and Bottjer 1995; Hallam and Wignall 1997; Wignall *et al.* 1998). Only one study of Early Triassic, level-bottom benthic palaeocommunity structure has been carried out, involving Lower Triassic (Nammalian, Spathian) carbonate strata in western North America. The average number of species in collections defining palaeocommunities in these shelfal settings is 13 (Schubert and Bottjer 1995; Bottjer *et al. in* Hart 1996). Comparison with data from Permian and later Triassic palaeocommunities indicates that species richness of these Early Triassic palaeocommunities is lower than typical later Palaeozoic or other Mesozoic palaeocommunities from equivalent environments (Schubert and Bottjer 1995; Bottjer *et al. in* Hart 1996).

Similarly, of the possible Bambachian megaguilds, only five are occupied in these Early Triassic palaeocommunities from western North America (Schubert and Bottjer 1995; Bottjer *et al. in* Hart 1996). This is a significant reduction from the 14 megaguilds typically found in Palaeozoic faunas, and also contrasts strongly with the 20 megaguilds commonly found in later Mesozoic–Cenozoic faunas (see Section 4.2.1) (Bottjer *et al. in* Hart 1996). Along with reductions in palaeocommunity species richness and occupation of Bambachian megaguilds, the end-Permian mass extinction also had a dramatic effect upon patterns of tiering (see Section 4.1.4). Studied Early Triassic palaeocommunities have only the 0 to +5 cm epifaunal tier present until the Spathian, when, with the reappearance of crinoids, the +5 to +20 cm tier again developed (e.g. Schubert and Bottjer 1995; Bottjer *et al. in* Hart 1996). Infaunal tiering, as indicated by trace fossils, was also strongly affected, with only the 0 to −6 cm and −6 to −12 cm tiers present in studied Lower Triassic stratigraphic sections (e.g. Schubert and Bottjer 1995; Bottjer *et al. in* Hart 1996; Twitchett 1999). By the Middle Triassic tiering appears to have recovered to levels found in the late Palaeozoic (see Section 4.1.4). General studies of trace fossils in the Dolomites, Spitsbergen, and western North America (Schubert and Bottjer 1995; Wignall *et al.* 1998; Twitchett 1999) typically show an increase in ichnogeneric diversity and the amount of bioturbation as recorded by ichnofabric indices through the Early Triassic, and this evidence has commonly been taken to indicate the presence of deleterious oxygen-deficient conditions during the recovery interval (e.g. Hallam and Wignall 1997; Wignall *et al.* 1998; Twitchett 1999). If sections in Spitsbergen show the oldest evidence for deeper infaunal tiering in the Early Triassic, as well as earlier Early Triassic faunas with appreciable diversity, then recovery from this mass extinction may have first begun in higher palaeolatitudes (Wignall *et al.* 1998).

The analysis of much of this palaeoecological data in a comparative fashion has shown that ecological conditions for this recovery interval (particularly the earlier part of the Early Triassic) were most like those of the Late Cambrian/Early Ordovician (Bottjer *et al. in* Hart 1996). Further analysis using palaeoecological levels shows that the Early Triassic recovery represents a major interval of ecological change, as great as any other in the Phanerozoic (see also Section 4.2.1). The effects of the end-Permian mass extinction include changes at the second, third, and fourth levels. The biggest changes are at the second level, including the loss of Bambachian megaguilds, a major shift in soft substrate shelf palaeocommunities from brachiopod-dominated (in the middle and late Palaeozoic) to bivalve-dominated, and a major restriction in metazoan carbonate build-ups (see also Section 4.2.1). Changes at the third level include reductions in epifaunal and infaunal tiering (see Sections 4.1.4 and 4.2.1), which occurred together with numerous small-scale fourth-level changes.

From the evidence outlined above, a temporal structure for the end-Permian mass extinction recovery inter-

val includes: (1) the mass extinction, which ended at the beginning of the Triassic; (2) the survival or lag, which lasted through the Griesbachian, and, depending upon geographical location, into some or all of the Nammalian; (3) the rebound, which probably began at different locations during various times in the Nammalian, indicated by the reappearance of gastropod Lazarus taxa, articulate crinoids, and other taxa in benthic palaeocommunities (e.g. Schubert and Bottjer 1995; Erwin and Pan *in* Hart 1996; Hallam and Wignall 1997; Wignall *et al.* 1998; Twitchett 1999); and (4) the expansion, which began with the start of the Middle Triassic.

Thus, a variety of features, such as the presence of opportunists, characterize the survival or lag, and the timing of the rebound seems to have differed depending upon geographical location. Still not resolved is why this recovery had such an unusually long duration. However, many studies of this recovery interval have focused on the effects of continued environmental stress linked to the cause of the mass extinction itself, such as anoxia or hypercapnia (e.g. Twitchett 1999; Woods *et al.* 1999). Most likely this prolonged biotic recovery from the end-Permian mass extinction was caused by the biotic effects of the mass extinction as well as harsh environmental conditions, both of which varied geographically and temporally in the Early Triassic (e.g. Woods *et al.* 1999).

Conclusions

The analysis of biotic recovery from mass extinctions provides fascinating glimpses of how the Earth's biota responds to severe stress. Taxonomic data have allowed the recognition and an initial understanding of these recovery intervals. Clearly, the detailed collection of palaeoecological data, in conjunction with additional taxonomic data, is needed to move the analysis of each Phanerozoic recovery interval forward. Our goal should be a general understanding of the biotic properties of these crisis intervals, with the ultimate aim of providing strategies to help manage the current biodiversity crisis.

References

Bottjer, D.J. (1998) Phanerozoic non-actualistic paleoecology. *Geobios* **30**, 885–893.

Boucot, A.J. (1983) Does evolution take place in an ecological vacuum? II. *Journal of Paleontology* **57**, 1–30.

Hallam, A. and Wignall, P.B. (1997) *Mass extinctions and their aftermath*. Oxford University Press, Oxford.

Hansen, T.A. (1988) Early Tertiary radiation of marine molluscs and the long-term effects of the Cretaceous–Tertiary extinction. *Paleobiology* **14**, 37–51.

Hart, M.B., ed. (1996) *Biotic recovery from mass extinction events*. Geological Society Special Publication no. 102.

Jablonski, D. (1986) Causes and consequences of mass extinctions: a comparative approach. In: D.K. Elliott, ed. *Dynamics of extinction*, pp. 183–230. John Wiley and Sons, New York.

Schubert, J.K. and Bottjer, D.J. (1992) Early Triassic stromatolites as post-mass extinction disaster forms. *Geology* **20**, 883–886.

Schubert, J.K. and Bottjer, D.J. (1995) Aftermath of the Permian–Triassic mass extinction event: paleoecology of Lower Triassic carbonates in the western USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* **116**, 1–39.

Sheehan, P.M. (1996) A new look at Ecologic Evolutionary Units (EEUs). *Palaeogeography, Palaeoclimatology, Palaeoecology* **127**, 21–32.

Twitchett, R.J. (1999) Palaeoenvironments and faunal recovery after the end-Permian mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology* **154**, 27–37.

Wignall, P.B., Morante, R. and Newton, R. (1998) The Permo-Triassic transition in Spitsbergen: $\delta^{13}C_{org}$ chemostratigraphy, Fe and S geochemistry, facies, fauna and trace fossils. *Geological Magazine* **135**, 47–62.

Woods, A.D., Bottjer, D.J., Mutti, M. and Morrison, J. (1999) Lower Triassic large sea floor carbonate cements: their origin and a mechanism for the prolonged biotic recovery from the end-Permian mass extinction. *Geology* **27**, 645–648.

2.3.11 Evolutionary Trends

D.W. McSHEA

Introduction

The increase in mean body size in horses from the Eocene to the Recent is an evolutionary trend. Underlying this trend was a particular 'dynamic', a tendency for size to increase rather than decrease in all or most equid lineages; in other words, a bias in the direction of size change (MacFadden 1986; McShea 1994). The distinction here is between a pattern, the trend in the mean, and its dynamic, or what might be called the rules of change in lineages that account for the pattern. In principle, the body-size trend could have been produced by a different dynamic. For example, if horses had originated at or near a size minimum—perhaps a lower limit on size imposed by selection—then as the group diversified, mean size would only have increased. The dynamic is different in that it involves only a local bias; that is, among the very smallest species (at their lower limit), no decreases occur, but at larger sizes, increases and decreases are equally frequent.

In palaeobiology, a major problem in the study of trends has been to discover the nature of the dynamic underlying them. The problem could be construed as a search for 'causes', but an explanation of a trend in dynamical terms is typically somewhat more general. That is, each dynamic is consistent with more than one factor that we would ordinarily call a cause. For example, a pervasive bias in the direction of body-size change in equid lineages could have been caused by external selection for large size, but in principle it could equally well have been caused by a developmental bias or constraint of some kind, one that was present in all or most horse lineages.

Central to the analysis of dynamics at this scale is a view of a species as a particle in a 'state space' (McKinney 1990), and a trend as the movement of one or more particles in state space. Figure 2.3.11.1(a) shows the trajectory of a species in a one-dimensional state space. In the figure, the state variable defining the space is unspecified, but in principle it might be any species-level property, such as average body size, average metabolic rate, probability of extinction, geographical range, or even the average location of a species in real space. The position in state space of the particle corresponds to the value of the state variable, and Fig. 2.3.11.1(a) shows how that value changes over time. In this view, origins of new lineages are represented by particle duplications (lineage bifurcations) as in Fig. 2.3.11.2(a). Implicit in the particle representation is a view of a species as a unified entity, an individual, one with properties that can be usefully studied independent of its population-level properties (McKinney 1990).

Trends occur at various taxonomic and temporal scales. Among the best studied in palaeobiology are: (1) trends in a single species-level lineage, usually on a time scale of millions of years (e.g. Fig. 2.3.11.1a); and (2) large-scale trends, or trends in groups of species, usually clades, on time scales ranging from tens of millions of years to the entire history of life (e.g. Fig. 2.3.11.2a).

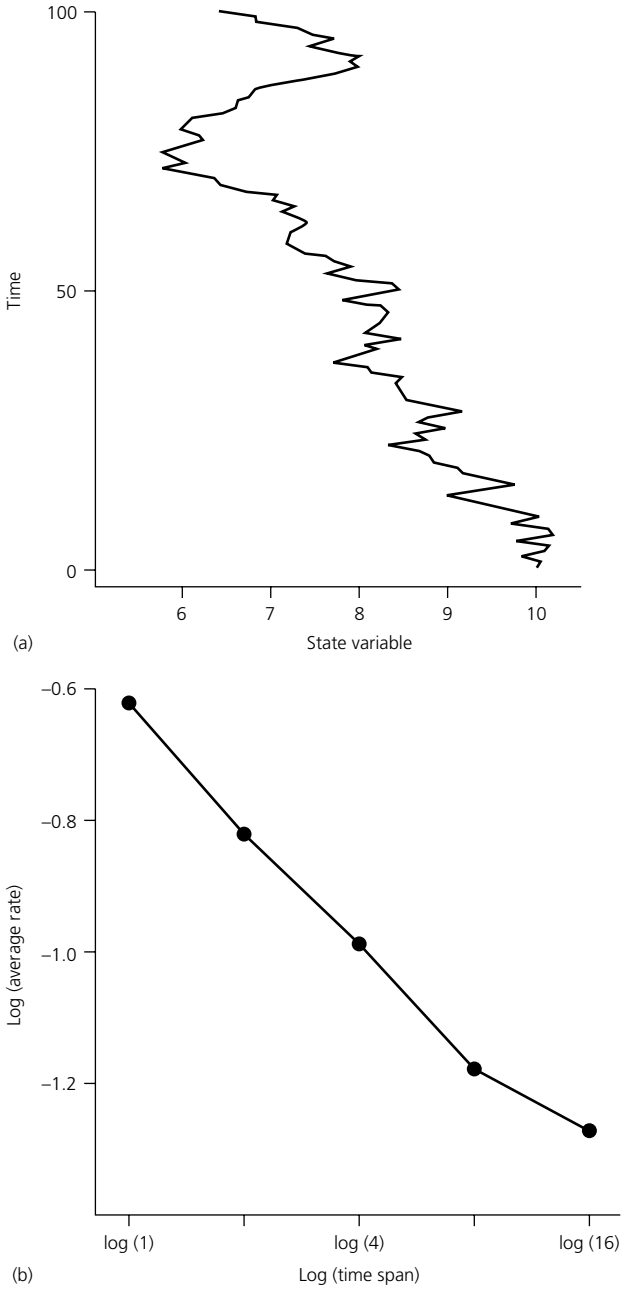

Fig. 2.3.11.1 (a) Random walk, over 100 time steps. (b) Log of average rate vs. log of time span. Average rate is computed for each time span as follows: the trajectory in (a) is divided up into non-overlapping units of a length equal to the time span; for a time span of 4, there are 25 such units. Then, a rate is computed for each unit as the net change in the state variable divided by the time span. Rates for all units are then averaged.

Single-lineage trends

Two issues have dominated research: (1) the problem of distinguishing trends produced by a simple dynamic from those produced by a complex dynamic, or random walks; and (2) the analysis of rates.

Random walks

Figure 2.3.11.1(a) shows a decreasing trend in some state variable. In the trajectory shown, both increases and decreases occurred, but on the whole, decreases predominated. If the figure were, say, a historical record of change in brain size for a fossil species, the temptation might be to look for a single, simple, and perhaps exogenous cause for the overall trend. For example, one plausible suggestion might be that reduction in brain size was selectively advantageous for this species over most of the time span shown, and that this

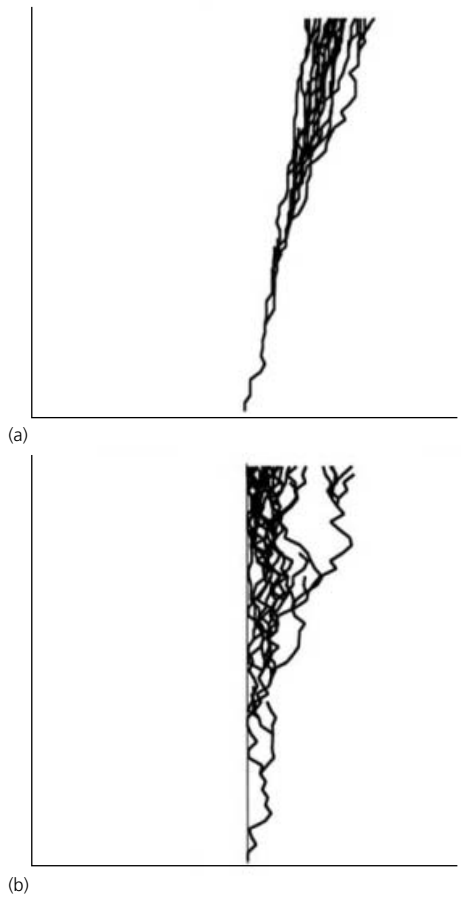

Fig. 2.3.11.2 Large-scale trends (horizontal and vertical axes as in Fig. 2.3.11.1a). (a) Driven trend. (b) Passive trend. See text for further explanation.

advantage—although occasionally overridden by other forces—produced a bias in the direction of change.

In fact, however, the figure was generated by a computer program in which the state variable was set initially at a value of 10, and then, in each time step, increased and decreased by a number chosen at random from the range –0.5 to +0.5. In other words, the underlying dynamic was an unbiased random walk, and the trend was entirely the result of chance. Actually—and for many, counter-intuitively—unbiased random walks commonly produce trends that are quite striking, such as this one, which raises the possibility that many trends in fossil data are the result of chance, and therefore require no single-factor explanation (Raup 1977).

The contrast here is between two underlying dynamics, biased and random, that seem to be capable of generating the same pattern. To put it another way, the contrast is between a simple and a complex dynamic. The bias dynamic is simple: some (stochastically) constant force or vector acts at all points in state space, causing lineages to decrease most of the time. The random dynamic might sound simple, but that is mainly because random numbers are easy to generate in many computer programs, or to look up in random number tables. However, in the present context, a random number generator is taken to model a complex process. In other words, randomness is understood as the outcome of multiple, diverse causes, complexly configured. Thus, for example, if a selection regime governed body-size change, and if that regime were highly variable on million-year time spans, then the expected trajectory for size might be a random walk.

Various methods have been developed for distinguishing biased from unbiased random walks in fossil data (Raup and Crick 1981; Bookstein 1988; Roopnarine *et al.* 1999). In one method, for example, the number of 'runs'—or sequences of jumps in state space occurring in the same direction (increase or decrease)—in a single-lineage trajectory is compared with the distribution of runs that would be produced by unbiased random walks of the same length (Raup and Crick 1981). Most of the tests that have been devised are fairly conservative, in the sense that the risk of a Type II error (i.e. concluding that data are consistent with an unbiased random walk when in fact they were produced by a weakly biased dynamic) is fairly high.

Rates

The rate problem has been especially interesting because of its relevance to a long-standing controversy. At issue is whether evolutionary change in single lineages is governed by some underlying dynamic which tends to produce continuous, gradual change throughout the lifetime of a species, or whether the dynamic is one that produces long periods of stasis punctuated by brief episodes of rapid change, i.e. punctuated equilibrium.

One analytical difficulty is that inferences about an underlying dynamic based on visual inspection of a pattern of rate changes can be misleading. For example, the first 75 steps of the trajectory in Fig. 2.3.11.1(a) might appear to be the result of a gradualistic underlying process. Following this period, a different dynamic might seem to dominate, one which tends to produce rapid change, accounting for the abrupt increase in the state variable. However, we know that the underlying dynamic is just an unbiased random walk, in other words, a dynamic that is inherently neither gradualistic nor punctuational.

One method for inferring dynamics from pattern takes advantage of a well-known inverse correlation between rate and time span (Gingerich 1993). Figure 2.3.11.1(b) shows this inverse relationship for the trend in Fig. 2.3.11.1(a). The figure is a plot of the log of the average rate of change in the state variable vs. the log of time span, for time spans of length 1, 2, 4, 8, and 16 (see Fig.

2.3.11.1 caption). The lower rates at longer time spans reflect the fact that longer time spans incorporate more reversals, and therefore show less net change per time unit. The slope of a regression of log(rate) against log(time span) is expected to be as follows: 0, when the underlying dynamic is one that produces a pure directional trend in the state variable, without reversal; –0.5, for a random walk; and –1, for a dynamic in which the state variable is highly stabilized, i.e. evolutionary stasis (Gingerich 1993). The reduced-major-axis slope in Fig. 2.3.11.1(b) is –0.55, close to the expectation for a random walk.

Other methods have been devised, including one which takes advantage of the fractal properties of random walks (Roopnarine *et al.* 1999).

Large-scale trends

For a clade, the pattern of interest is directional change in the clade as a whole, as measured by some summary statistic. For example, Fig. 2.3.11.2(a) shows an increase in the mean, i.e. in the average location in state space of all lineages existing at any given time. Likewise, there is an increase in the maximum (the location in state space of the right-most lineage at any given time) as well as in the minimum, the mode, and the median.

Figure 2.3.11.2(a) was generated by a computer program in which a clade begins as a single species, a single lineage, at some location in state space. In each time step, that lineage had a fixed probability of branching (i.e. generating a new species) and a fixed probability of becoming extinct. All later-arising lineages had the same probabilities. Also, in each time step, lineage movement was governed by a bias, so that the probability of increase (moving right in state space) was substantially greater than the probability of decrease (moving left).

Figure 2.3.11.2(b) shows a large-scale trend generated by the same program but using different parameter values, thus producing a different dynamic. Over most of the state space, each lineage followed an unbiased random walk, as in Fig. 2.3.11.1(a), but the state space also contained a boundary, a lower limit on the movement of lineages, shown as a vertical line in Fig. 2.3.11.2(b). That is, decreases that would have moved existing lineages, or created new ones, to the left of the boundary were forbidden (see McShea 1994 for details of the computer model). For example, if the state variable were morphological complexity, and the figure represented the diversification of life as a whole, a lower bound might represent a design limitation, the complexity of the simplest possible species. Such boundaries have been proposed to explain large-scale trends in a number of state variables (Fisher 1986; McKinney 1990; McShea 1994; Gould 1996).

Another way to describe the difference in dynamic between the systems in Fig. 2.3.11.2(a) and Fig. 2.3.11.2(b) is in terms of distributions of dynamical rules (McShea 1998). In Fig. 2.3.11.2(a), all lineages throughout the state space were governed by a bias; in other words, the 'bias-rule' was distributed homogeneously throughout the state space, applying equally to all lineages at all times. In Fig. 2.3.11.2(b), the distribution was heterogeneous: no bias was present over most of the state space, but all lineages reaching a certain region of state space were blocked; in other words, 'blocking rules' operated there.

Trends in which the dynamic, or underlying rule distribution (also called a trend 'mechanism'; see McShea 1994), is homogeneous, such as Fig. 2.3.11.2(a), are called 'driven', while those in which it is heterogeneous, as in Fig. 2.3.11.2(b), are 'passive' (McShea 1994). The trends in both figures might be called classic cases, in that the state-space distributions of dynamical rules governing them are simple and therefore might be fairly common in evolution.

Notice that in the model above, the assumption is that change is anagenetic, occurring between speciation events as well as during them; and that a similar model, in which change is concentrated at speciation events (i.e. a model based on punctuated equilibrium) could have been used to make the same points.

Pattern vs. dynamics

As for single-lineage trends, a major problem has been to infer some aspect of dynamics from pattern. However, for the most part, no simple general relation exists; in other words, the same pattern can be produced by very different dynamics. For example, a pattern similar to that in Fig. 2.3.11.2(b) might be produced by an extinction boundary, an abrupt increase in extinction probability at one point in state space, rather than by blocking rules. (Further, any given rule distribution may have any of a number of different underlying causes; for example, a blocking-rule boundary might be the result of either developmental constraints or external selection.)

Still, some generalizations are possible, especially concerning the dynamics underlying changes in minima and maxima. These statistics have been of special interest in the analysis of large-scale trends (Trammer and Kaim 1999), at least partly because the extremes in any distribution are among its most striking features (Gould 1996). Examples include the increase in maximum 'hierarchical depth' for life as a whole, a trend that has resulted from the occasional advent of higher levels of organization (e.g. the transitions from free-living eukaryotic cell to multicellular organism to colony, and so on), and the increase over the history of life in the body size of the largest organism in existence. (In contrast, the hierarchical minimum and the size minimum

are thought to have remained roughly constant; see Gould 1996.)

In the discussion that follows, the assumption is that the underlying dynamic is constant—or at least stochastically constant—in time. Of course, for certain clades, or at certain times, this would clearly not be a reasonable assumption. For example, the massive changes in external selection regime that doubtless accompany mass extinctions might well produce a wholesale reorganization of the dynamic in many clades.

First, consider what might be called a null model of clade evolution. In such a model, the state space would be one in which there were no biases, no boundaries, and uniform extinction and speciation probabilities. In such a space, if diversity increases (i.e. if speciation probability is greater than extinction probability), the maximum would be expected to increase and the minimum to decrease, symmetrically (Fig. 2.3.11.3c; see Trammer and Kaim 1999). Conversely, if diversity decreases, the extremes should draw together (Fig. 2.3.11.3g).

Notice, however, that if diversity increases, a simple pattern of consistent increase in the maximum by itself reveals very little about the underlying dynamic. Indeed, such a pattern is consistent with either a driven (Fig. 2.3.11.3a) or passive (possibly Fig. 2.3.11.3b) dynamic, and also with the null model (Fig. 2.3.11.3c). Similarly, a consistently decreasing minimum would not be very informative (Fig. 2.3.11.3c,f). Finally, if diversity decreases, a pattern of consistent decrease in the maximum (Fig. 2.3.11.3g,h,i) or increase in the minimum (Fig. 2.3.11.3d,g) would by itself reveal little about dynamics.

However, inconsistent behaviour of maxima and minima (not shown) may be more telling: for example, if

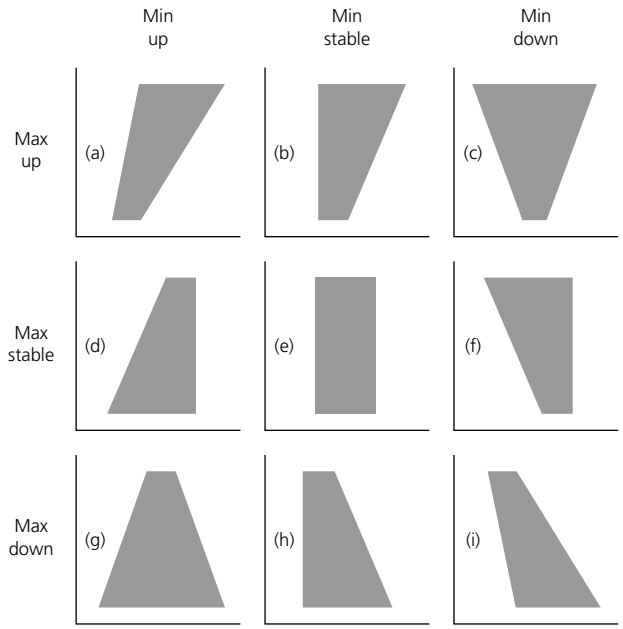

Fig. 2.3.11.3 Nine possible patterns of change in minima and maxima in large-scale trends (horizontal and vertical axes as in Fig. 2.3.11.1a). The trapezoidal shaded regions show how the range—from minimum to maximum—in state space occupied by a clade changes over time. Diversity increases in (a), (b), (c), and (f); it decreases in (d), (g), (h), and (i); and it remains the same in (e). (Based on a figure in Trammer and Kaim 1999.)

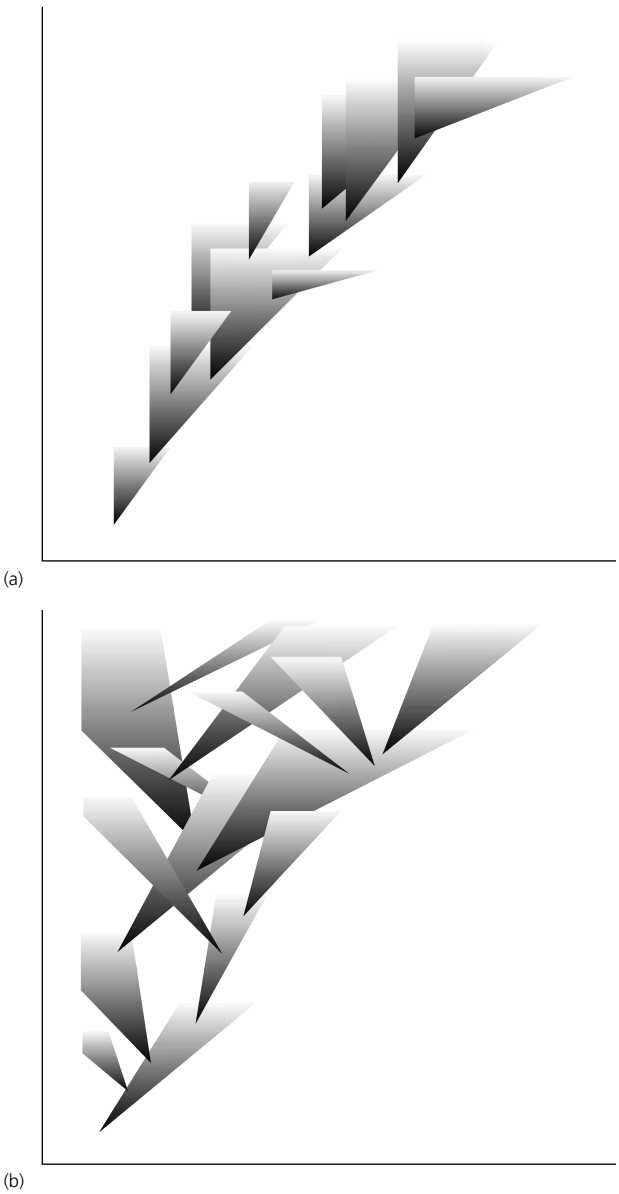

Fig. 2.3.11.4 Two cases in which trend dynamic differs between scales (horizontal and vertical axes as in Fig. 2.3.11.1a). In both, the small wedges represent diversifying clades. Only the initial diversification of each is shown; thus, the upper edge of each does not necessarily correspond to the extinction of the clade. (a) Driven at the large scale, passive at the small scale. (b) Passive at the large scale, driven at the small scale.

the maximum increases only initially and then levels off, an inhomogeneous dynamic might be a reasonable inference, perhaps an upper boundary of some kind.

Finally, when diversity increases, a rising minimum can be informative. In Fig. 2.3.11.3(a), the rising minimum suggests a driven trend. Importantly, however, a stable minimum, as in Fig. 2.3.11.3(b), does not necessarily indicate passive, because a weakly driven dynamic can produce the same pattern (McShea 1994). (Certain caveats are relevant here, and other methods for distinguishing passive and driven have been devised; see McShea 1994, 1998.)

A final cautionary point is worth making about scale dependence. In a large-scale trend, different dynamical rules and rule distributions may occur at different scales within a clade. For example, Fig. 2.3.11.4(a) shows a case in which the dynamics within the smaller subclades are all passive, but the dynamic at the scale of the entire clade is driven. Figure 2.3.11.4(b) shows the converse case. Thus, for example, in principle, a discovery that changes in relative brain size within various mammalian taxa were mainly driven would not contradict a finding that the increase in mammals as a whole was passive.

References

Bookstein, F.L. (1988) Random walk and biometrics of morphological characters. *Evolutionary Biology* **23**, 369–398.

Fisher, D.C. (1986) Progress in organismal design. In: D.M. Raup and D. Jablonski, eds. *Patterns and processes in the history of life*, pp. 99–117. Springer-Verlag, Berlin.

Gingerich, P.D. (1993) Quantification and comparison of evolutionary rates. *American Journal of Science* **293A**, 453–478.

Gould, S.J. (1996) *Full house: the spread of excellence from Plato to Darwin*. Harmony Books, New York.

MacFadden, B.J. (1986) Fossil horses from 'Eohippus' (*Hyracotherium*) to *Equus*: scaling, Cope's Law, and the evolution of body size. *Paleobiology* **12**, 355–369.

McKinney, M.L. (1990) Classifying and analysing evolutionary trends. In: K.J. MacNamara, ed. *Evolutionary trends*, pp. 28–58. University of Arizona Press, Tucson, Arizona.

McShea, D.W. (1994) Mechanisms of large-scale trends. *Evolution* **48**, 1747–1763.

McShea, D.W. (1998) Dynamics of diversification in state space. In: M.L. McKinney, ed. *Biodiversity dynamics*, pp. 91–108. Columbia University Press, New York.

Raup, D.M. (1977) Probabilistic models in evolutionary paleobiology. *American Scientist* **65**, 50–57.

Raup, D.M. and Crick, R.E. (1981) Evolution of single characters in the Jurassic ammonite *Kosmoceras*. *Paleobiology* **7**, 200–215.

Roopnarine, P.D., Byars, G. and Fitzgerald, P. (1999) Anagenetic evolution, stratophenetic patterns, and random walk models. *Paleobiology* **25**, 41–57.

Trammer, J. and Kaim, A. (1999) Active trends, passive trends, Cope's Rule and temporal scaling: new categorization of cladogenetic body size changes. *Historical Biology* **13**, 113–125.

2.4 Patterns of Diversity

2.4.1 Biodiversity through Time

M.J. BENTON

Biodiversity today

Estimating modern diversity

Estimates of the present diversity of life range over at least an order of magnitude, from perhaps 2–3 million species at the lower end, to 30–100 million at the upper end. The lower estimates represent summaries of the number of species that have actually been documented. It is estimated (May 1990), for example, that some 1.7–1.8 million species of modern microbes, plants, and animals have been named so far by systematists, and that figure must be a minimum estimate of current biodiversity. Even this assertion, however, must be considered carefully, before proceeding. If synonymy (i.e. the error of naming as new a species that has already been named) is rampant, that total of 1.8 million may be an overestimate.

The roster of named living species clearly includes many synonyms, and the synonymy rate may be as much as 20–40%, based on close study of particular

groups. Synonymy is an inevitable result of the way in which systematists name new species, representing a level of expected error. When erecting a new species, a systematist attempts to establish unequivocally that the purported new form has never been named before, but it is possible to overlook a previous publication, perhaps in an obscure journal, in a language unfamiliar to the systematist, or presented in such a way that its identity is difficult to determine (incomplete description or poor illustrations). Hence, the total of 1.8 million named modern species might be reduced to 1.4 million, if all synonyms were recognized and deleted (Wilson 1992).

Counter to the synonym problem, however, is the constant accretion of newly described species. Each year, on average, systematists add one or two new species of mammals and three new species of birds to the lists (based on estimates of taxonomic activity from 1900 to 1975) as well as dozens of newly named microbes, fungi, plants, and marine animals, and some 7250 new species of insects (Wilson 1992).

The collector curve

These rates of new species descriptions provide one way to estimate the actual diversity of life on Earth. If the additions are the same each year, the pattern of increase would be linear. However, the pattern may be more complex. It could be argued, for example, that the discovery of new species would follow a collector curve, i.e. a pattern of rapid rise when new species were being discovered all the time, followed by a slowing-down of the rate as the number of described species approaches the true diversity (Fig. 2.4.1.1). For birds or mammals, it is likely that the levelling-off phase, the asymptote, was reached about 1900 (Fig. 2.4.1.1a), and that the current slow rate of discovery of new species really means that virtually all species on Earth have been discovered. This evidence could lead to a modest estimate of perhaps 3 million species for true current biodiversity. However, a little reflection suggests that this comfortable impression is probably very far from the truth.

It is wrong to extrapolate from the groups of living organisms that are most fully documented, such as birds and mammals. For insects, microbes, fungi, parasites, meiofauna, deep-sea organisms, and many others, taxonomists find new species wherever they look. If a taxonomist of bacteria takes a random soil sample, he finds many hundreds of previously unrecognized species; if a marine biologist scans a sample of mud scraped from the deep ocean floor, she may find dozens of undescribed species. For these groups, the rates of discovery and description depend only on the time and effort expended by taxonomists. This means that it is impossible to predict ahead when the curve will show an asymptote (Fig. 2.4.1.1b), and consequently final totals

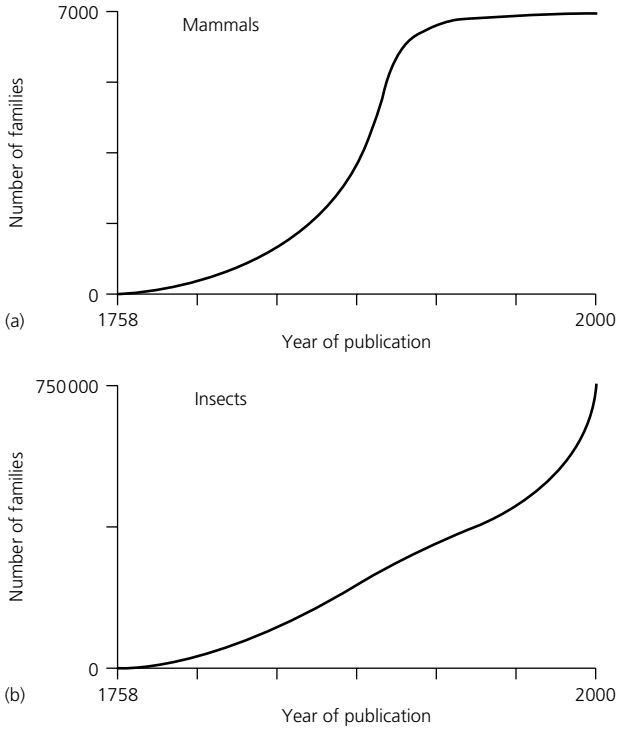

Fig. 2.4.1.1 Collector curves and the estimation of total biodiversity. (a) For well-known groups, such as birds or mammals, apparently nearly all species that exist have been named and described, and the collector curve shows an asymptote to the true biodiversity. (b) For incompletely known groups, such as insects, bacteria, fungi, or parasitic organisms, the rate of discovery is still high, and it is impossible to predict when the rate will slow down and approach the actual total.

for many groups cannot be estimated. These little known groups are highly speciose, and their current diversities must far outweigh those of well-known groups such as birds and mammals. Regrettably, then, estimates of actual global biodiversity based on current records can only work for heavily studied groups like birds and mammals, but not for vast sectors of life where taxonomic work has barely begun.

Extrapolation from intensive local sampling

Biologists have tried another approach in estimating modern biodiversity. For highly speciose groups, it might be more appropriate to carry out a detailed survey in one spot on Earth, find the maximum diversity, and then extrapolate worldwide. A well-known experiment concerns tropical rain forest beetles (Erwin 1982). The entire arthropod fauna was sampled from the canopy of the tree *Luehea seemannii* from Central and South America. This was done by setting 'bug bombs' under the selected trees, devices that pump powerful insecticide. All the dead arthropods which fell to the ground

were collected and classified. Erwin estimated that there are 163 species of beetles living exclusively in the canopies of *L. seemanni*. There are about 50 000 tropical tree species around the world, and if the numbers of endemic beetle species in *L. seemanni* is typical, this implies a total of 8.15 million canopy-dwelling tropical beetle species in all. This figure excludes forms that live in several tree species. Beetles typically represent about 40% of all arthropod species, and this leads to an estimate of about 20 million tropical canopy-living arthropod species. In tropical areas, there are typically twice as many arthropods in the canopy as on the ground, giving an estimate of 30 million species of tropical arthropods worldwide. This estimate came as a considerable surprise when it was published: 30 million species of tropical arthropods must imply a global diversity of all life in the region of 50 million. Some wild-eyed biologists even talked of figures of 100 million or more!

However, mature reflection has suggested that Erwin's (1982) estimate was closer to the truth than more conservative estimates of 2–5 million (May 1990; Wilson 1992). Similar extrapolation exercises have been performed for deep-sea organisms, microbes, fungi, and parasites, and they all point to total global biodiversities of 20–100 million. Such estimates are astounding, and they have profound consequences. Should systematists give up the endeavour to describe and name all species since they will never finish the task? Should governments employ many more systematists in order to do the work properly? How can conservationists and planners begin to estimate the effects of pollution and other human activities on biodiversity since no one has the faintest idea how many species exist today, nor what they are, and where they are?

Biodiversity through time—patterns of increase

Life is unexpectedly diverse today. Indeed, it is assumed that life is more diverse today than it ever has been. This seems in some ways obvious, and yet it could also be construed as extraordinary vanity, somehow akin to the view that all of evolution was planned to lead to human beings, that somehow this instant in the vast span of time is the most important of all. However, it is evident that all living organisms, and all organisms known as fossils, derive from a single common ancestor (based on the evidence of shared complex characters, such as the DNA–RNA system of inheritance, homeobox genes, and the like). That common ancestor, the single species that gave rise to all of life, existed some 3500–3800 million years ago. Biodiversity has, then, expanded from one species to some 5–50 million species.

There are many ways to go from one species to many, and these can be expressed simply in terms of three mathematical models, represented by a straight line, an exponential curve, and a logistic curve, firstly as an uninterrupted increase (Fig. 2.4.1.2a), and secondly with some mass extinctions superimposed (Fig. 2.4.1.2b).

The linear model represents additive increase: simply the addition of a fixed number of new species in each unit of time. (The increase in this example, and the others, is a net increase, i.e. true increase minus extinctions.) In terms of an evolutionary branching model, additive increase would mean that, through time, speciation rates have declined, or extinction rates have increased regularly at a rate sufficient to mop up the excess speciations. The implied decline in the rate of evolution in the linear model comes about simply because

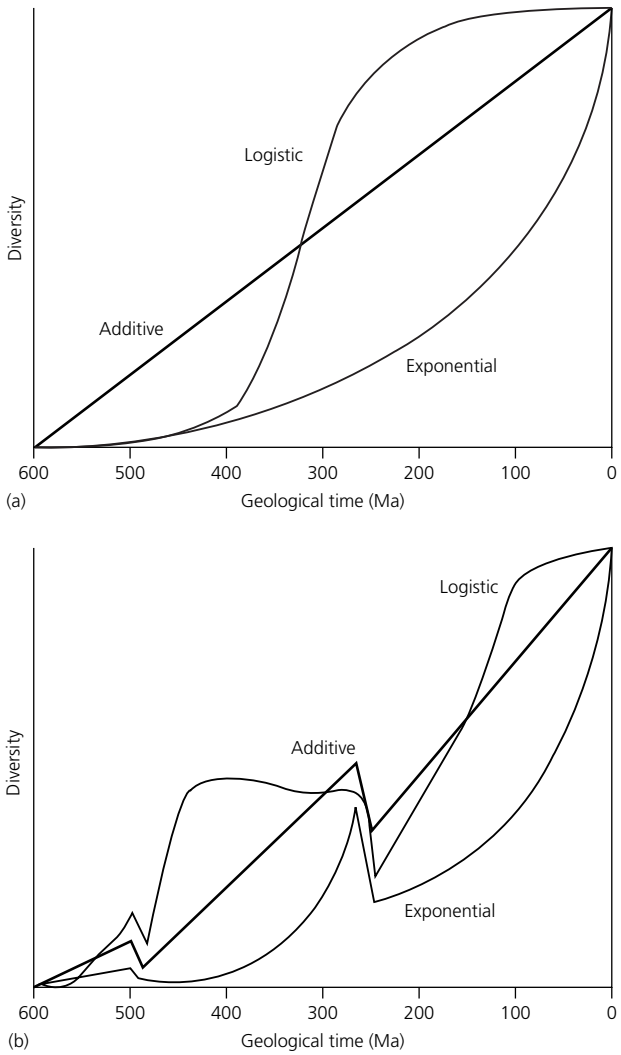

Fig. 2.4.1.2 Theoretical models for the diversification of life: (a) in the absence of major perturbation; and (b) with two mass extinctions superimposed. In each case, the upper curve is the logistic or equilibrium model, the middle curve is the additive or linear model, and the lower curve is the exponential model.

the total number of species is increasing regularly, and yet the *rate* of increase across the board remains fixed; hence, for any individual evolutionary line, the rate or probability of splitting (speciating) must decline. Such a model has generally been rejected as improbable.

The exponential model is more consistent with a branching mode of evolution. If speciation and extinction rates remain roughly constant, then there will be regular doubling of diversity within fixed units of time. A steady rate of evolution at the level of individual evolutionary lines scales up to an exponential rate of increase overall since total diversity is ever-increasing. This model has been applied to the diversification rates of individual clades, and to the diversification of life in general (Benton 1995; Hewzulla *et al.* 1999).

The logistic model involves one or more classic S-shaped curves, each consisting of an initial period of slow diversity increase, a rapid rise, a slowing of the rate of increase as a result of diversity-dependent damping factors, and then a plateau corresponding to a limiting or equilibrium value. The logistic model has been used to explain patterns of diversification of marine organisms (Sepkoski 1984) and of plants.

There is clearly no consensus on which model best explains the diversification of major sectors of life through time, nor on whether all patterns of diversification adhere to the same model of increase. The choice of model is important since each makes profoundly different claims about evolution.

A different approach to the question of diversification through time has been to attempt to estimate the sum total of all species that have ever existed. Three lines of reasoning suggest that 2–4% of all species of plants and animals that have ever existed are alive today (Sepkoski 1992; May 1994):

1 The first argument is based on an assumed pattern of species diversity increase, and the known average duration of a species before it becomes extinct. If species diversity increased roughly linearly (additive model) through the Phanerozoic, and average species duration is 5–10 myr, then living species represent 2–4% of those that existed through the past 600 myr.

2 The second argument is based on the diversification of insects over the past 450 myr. If the average duration of an insect species is 10 myr, and the group has diversified linearly, then 5% of all terrestrial species that ever existed are alive today.

3 The third argument is based on preservability of the fossils. Some 250 000 species of fossil marine animals have been named, similar to the total number of known marine animal species alive today (200 000). Allowing for non-preservation of soft-bodied organisms, and other losses, this could also represent only 2–4% of the total number of fossil species (Sepkoski 1992).

In these discussions, it has only been possible to examine patterns of diversification for macroscopic organisms, typical plants and animals. Microbes are excluded, because almost nothing is known of their current diversity, and even less is known of their fossil record. If 2–4% of all species that ever existed are alive today (3–50 million), there must have been some 75–2500 million species in the past.

Biodiversity through time—land and sea compared

There are major differences between the patterns of diversification on land and in the sea, and the history of life in each realm may have been rather different. Today, about 85% of described species of plants and animals live on land, and the main groups (plants, arthropods, vertebrates) have reached their present great diversity in the past 450 myr. Plants and animals have been evolving in the sea since at least 600 Ma, and the fossil record is dominated by marine species, which make up some 95% of all described forms. This dominance of marine forms is partly accounted for by the fact that virtually the only organisms known from the Vendian and early Palaeozoic (600–450 Ma) are marine, and that the early history of life on land appears to have occurred at relatively low diversities. Also, fossils in certain marine environments are more likely to be preserved than those in many continental settings. The observation that life on land today is apparently five to six times as diverse as life in the sea, largely because of the insects, could be an artefact reflecting the greater amount of time devoted by systematists to continental than to marine organisms. However, if this difference is even partly correct, then it would imply a much more rapid diversification on land than in the sea.

In studies of the diversification of marine animal families (Fig. 2.4.1.3a), there is evidence for a short plateau in the Cambrian (lasting ≈40 myr), and a longer one from the Ordovician to the Permian (≈250 myr). This is followed by a long phase (250 myr) of near-exponential increase in diversity through the Mesozoic and Cenozoic, the rising element of a third logistic curve, which shows a hint of a slow-down in the last 25 myr or so, suggesting that a third plateau level may be achieved 125 myr in the future (Sepkoski 1984).

Marine invertebrate diversification has been explained (Sepkoski 1984) as the succession of three major phases of evolution, in which broad assemblages of different phyla ('evolutionary faunas') dominated the oceans, and were then replaced. The Cambrian fauna diversified exponentially at first, and then diversification slowed as the equilibrium level of 85 families was approached. The exponential diversification of the Palaeozoic fauna then began in the Early Ordovician, reaching an equilibrium diversity of 350 families, and

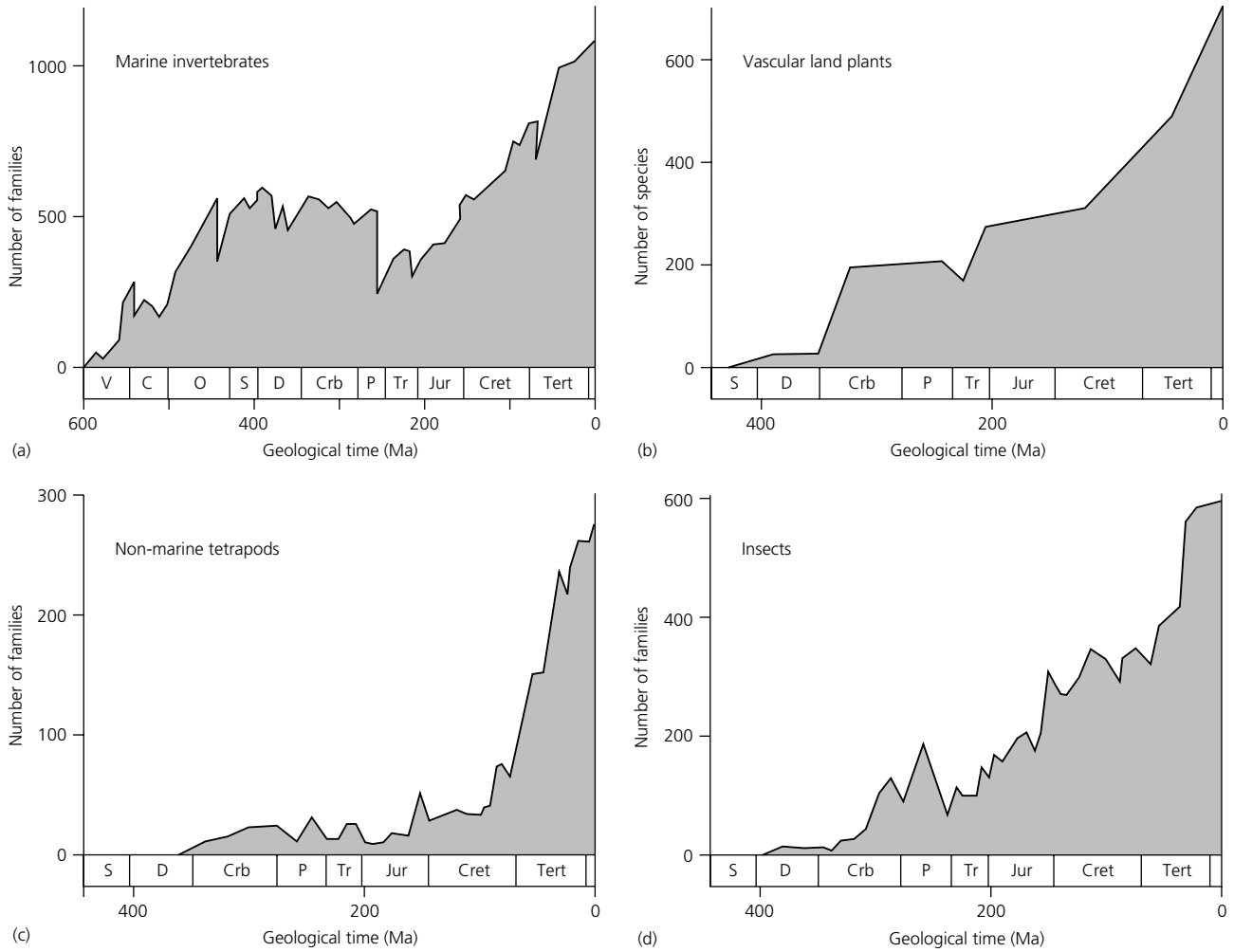

Fig. 2.4.1.3 Patterns of diversification of families of: (a) marine invertebrates; (b) vascular land plants; (c) non-marine tetrapods; and (d) insects. (Based on Sepkoski 1984; Benton 1985; Niklas *et al*. 1985; Labandeira and Sepkoski 1993.)

largely supplanting the Cambrian fauna. Finally, after the end-Permian mass extinction, which reduced the global diversity of the Palaeozoic fauna dramatically, the Modern fauna continued and accelerated its long-term rise in diversity.

In studies of the diversification of vascular plants (Fig. 2.4.1.3b), an equilibrium interpretation has also been given (Niklas *et al*. 1985). There was a succession of major baupläne of plant types: early vascular plants in the Devonian; lycopods, ferns, conifers, and others in the Carboniferous to Permian; gymnosperms in the Triassic to Jurassic; and angiosperms from the Cretaceous onwards. There was evidence for declining speciation rates and increasing species durations during each of the first three radiations, as the new set of clades partially replaced the old. Each new radiation led to an increase in total global diversity, while the diversity of the preceding floras declined. Angiosperms apparently continue to diversify at a high rate. It is hard to identify plateaus in land-plant species diversification, and it is hard to find evidence for logistic models of diversification. Equally, the total curve of species diversities through time is not obviously exponential and, if anything, the pattern appears to suggest linear increase in diversity through time.

The diversification of continental tetrapod families (Fig. 2.4.1.3c) appears to correspond to an exponential model of increase (Benton 1985). Diversity levels remained low, at some 30–40 families, during the late Palaeozoic and much of the Mesozoic. They then rose to about 100 families at the end of the Cretaceous and, after recovery from the end-Cretaceous (K–T) extinction event, familial diversity increased rapidly towards 330 families, and it shows no sign of a slow-down. The pattern of diversification may be dissected into successive radiations of three global clade associations: basal tetrapods (formerly termed 'labyrinthodont' amphibians) and synapsids ('mammal-like reptiles') in the late

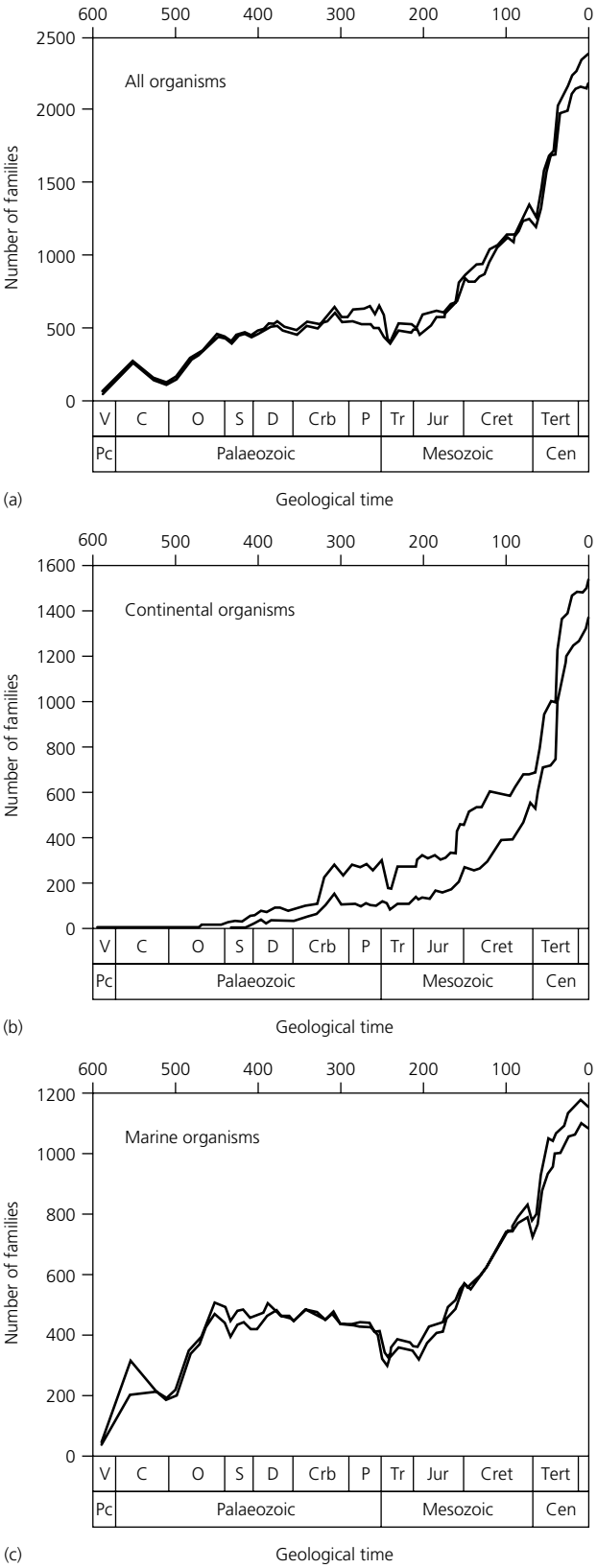

Fig. 2.4.1.4 Patterns of the diversification of life through time in terms of changes in numbers of families extant per stratigraphic stage, plotted for: (a) all organisms; (b) continental organisms; and (c) marine organisms. In each graph, a maximum and minimum is shown, based on a combination of stratigraphic and habitat-preference information. The minimum measure includes only families recorded as definitely present within each stratigraphic stage, or as definitely spanning that stage, and only families designated as restricted solely to the marine or continental realm. The maximum measure includes also all doubtful stratigraphic attributions of families, and all equivocal and shared habitat designations. The sum of minimum measures for continental and marine organisms is equal to the minimum measure for all taxa together. The sums of maximum measures, however, do not equal the maximum measure for all taxa because families with equivocal environmental assignments, and those which occur in both marine and continental settings, are counted as both marine and continental. (Based on Benton 1995.)

Palaeozoic; archosaurs (dinosaurs, pterosaurs, crocodilians) in the Mesozoic; and lissamphibians (frogs and salamanders), lepidosaurs (lizards and snakes), birds, and mammals from the Late Cretaceous to the present day. These clade associations replace each other, and are associated with ever-higher global familial diversity levels, but it is difficult to fit logistic curves to any of the associations.

The diversification of insects (Fig. 2.4.1.3d) was also apparently exponential, especially in the Mesozoic portion of the curve (Labandeira and Sepkoski 1993). This suggests that insects have had a long and continuous pattern of expansion, perhaps slowing somewhat during the Tertiary. This may indicate that insect diversity is approaching an equilibrium level now.

Recent plots of the diversification of families of marine, continental, and 'all' life (Fig. 2.4.1.4) founded on a new database (Benton 1993) confirm these varying models for diversification. The continental curve (Fig. 2.4.1.4b), dominated by tetrapods, insects, and land plants, is exponential. The marine curve (Fig. 2.4.1.4c) retains a Palaeozoic plateau level, and appears to show a slowing-down in diversification towards the Recent, which may indicate that marine diversity levels today are approaching an equilibrium level. The curve combining all marine and continental families (Fig. 2.4.1.4a) could be interpreted as a single poorly fitting exponential curve (Hewzulla *et al.* 1999), but the Palaeozoic plateau, reflecting the contribution of marine invertebrates (compare Fig. 2.4.1.4c), cannot be explained readily. The pattern could be explained equally well by a series of logistic curves, although the post-Palaeozoic portion is harder to fit than the Palaeozoic.

There may be fundamental differences between marine and continental life. Rates of taxonomic turnover in marine invertebrates declined through the Phanerozoic after the initial rapid Cambrian radiation, while vascular land plants show increasing rates of turnover through time (Valentine *et al.* 1991). Terrestrial vertebrates show intermediate patterns. The suggested explanation is that adaptive space was filled early on in the sea, while land plants (and possibly vertebrates) have continued, and may still continue, to conquer new ecospace. The persistence of opportunities for expansion on land may reflect the later onset of diversification here than in the sea, and the fact that new groups of plants invaded unstable habitats and modified them.

Explanations for patterns of diversification

Logistic and exponential models for the diversification of life could be compared directly. However, there is a slight ambiguity in attempting this since the initial phase of a logistic curve is essentially exponential. The key distinction is between equilibrium and non-equilibrium (or expansion) models. The former imply the existence of global equilibria in diversity, while expansion models assume that there is no ceiling to the diversity of life, or at least that such a ceiling has yet to be reached.

Equilibrium models

Equilibrium models for the expansion of the diversity of life were based on an influential body of ecological theory. Logistic modelling of global-scale data on diversification assumes: (1) interactions among species within clades; (2) interactions between clades; and (3) global equilibrium levels. Many studies show that clades may radiate initially at exponential rates, but that the rate of diversification slows at a certain point as a result of diversity-dependent phenomena, such as competitive exclusion, increased species packing, and reduction of species ranges (Sepkoski 1984, 1996). This style of reasoning follows explicitly from classical experiments in competition where the increase of one population suppresses another that depends on the same limiting resource. An initial exponential increase of the successful population is followed by a plateau when the species begins to deplete the limiting resource (usually food); this corresponds to the local carrying capacity.

The pattern of diversification of marine families (Fig. 2.4.1.3a) has been interpreted (Sepkoski 1984, 1996) in terms of a three-phase logistic model which represents the behaviour of the three evolutionary faunas: Cambrian, Palaeozoic, and Modern. The replacing 'faunas' are said to have been characterized by the ability to penetrate ever-wider sets of niches, and hence to achieve higher diversities. There is some evidence in favour of this idea; for example, later marine animals could burrow deeper, form more complex reefs, and capture prey in ever more ingenious ways. The equilibrium models could be interpreted simply in terms of large-scale competition between major clades, with bivalves outcompeting brachiopods, mammals outcompeting dinosaurs, and so on. Despite its popular appeal, such a view has been generally rejected (Benton 1987; see Sections 2.3.3 and 2.3.4). Sepkoski (1996) attributed the patterns of waxing and waning of clades to diffuse competition between them at the species level, where species in one clade are generally competitively superior to those in another.

A key assumption of logistic modelling is that equilibrium levels exist, i.e. there are steady-state diversities at which speciation and extinction rates are balanced. In the case of global diversification patterns, limiting processes could affect both extinction and origination rates. Origination rates may be more diversity dependent (Sepkoski 1996), however, because: (1) filling of niches could limit opportunities for new species to arise and become established; (2) additional species may intensify diffuse competition and create new directed competition, causing exclusion and thus possible extinction of some species; and (3) increased species packing may cause average local population sizes to be reduced, leaving some rarer species more prone to extinction by adverse environmental challenges.

There are three areas of concern with equilibrium models:

1 There is no independent evidence for equilibria, i.e. for fixed carrying capacities, on the Earth today. In evolutionary terms, equilibrium diversities imply that all available resources are in use and all ecospace is filled. If a new species originates, it must displace a pre-existing one. However, observations of cases where previously isolated floras and faunas come into contact suggest that species are just as likely to insinuate (i.e. enter new niches) and not cause extinction of other taxa.

2 Multiple logistic models imply predictable outcomes of interactions between members of the different 'faunas', i.e. that members of one group will generally succeed where those of another will fail. Where major biotic replacements have been investigated, one group is more likely to disappear due to an extinction event (Benton 1987; see Section 2.3.4) than as a result of interactions.

3 The diversification of the Modern fauna seems more prolonged and slower than predicted by a logistic model. The rising phase of the logistic curve has lasted for 250 myr, with some evidence of a slow-down towards the present. If there is no current plateau, then it would seem that in the second half of the Phanerozoic, the

best-known part of the fossil record, the logistic rules have been forgotten.

Expansion models

The alternative to equilibrium is expansion. Are the aggregate patterns, or at least some of them (Figs 2.4.1.3 and 2.4.1.4), the result of unconstrained expansion? Certainly, some clades (such as insects, angiosperms, birds, and mammals) seem to continue radiating linearly or exponentially for many tens or hundreds of millions of years. Such ever-expanding patterns imply that these groups are highly successful and adaptable. The overall patterns of diversification (Fig. 2.4.1.4) incorporate the numerous constituent clades, some expanding, others diminishing, and yet others remaining at constant diversity at any particular time. From an expansionist viewpoint, there is no prediction of how the individual clades affect each other. New global diversity levels may be achieved by combinations of new adaptations, habitat changes, and extinction events. In the past 250 myr, the diversification of life has been dominated by the spectacular radiations of certain clades, both in the sea (decapods, gastropods, teleost fishes) and on land (insects, arachnids, angiosperms, birds, mammals). There is little evidence that these major clades have run out of steam, and nothing to indicate that they will not continue to expand into new ecospace.

Exponential increase could imply that diversification would last forever. Presumably there is a limit to the numbers of families, or other taxa, that can inhabit the Earth at any time: such a limit would be caused not least by the amount of standing room on the Ark. If a limit of living space were approached, ever-smaller organisms would presumably be favoured by selection. Equally, as has happened so many times during evolution, organisms would take unexpected measures to survive, for example, by occupying the air, burrowing into sediments and, in the case of some bacteria, living deep within the Earth's crust. With size reduction, the ultimate limit to the diversification of life might then become the availability of the chemical components of life, principally carbon.

Equilibrium or expansion?

Five observations might provide a test for distinguishing equilibrium and expansion models of the diversification of life:

1 There was an evolutionary explosion of marine animals during the Early Cambrian, and diversification rates slowed after this initial exponential rise. This strongly suggests a logistic/equilibrium explanation.

2 The radiation of life on land, and of certain major marine and continental clades, appears to have followed an exponential pattern, and there is no sign of any slowing down in the rate of increase, nor of the occurrence of any equilibrium levels. These radiations strongly suggest patterns of unfettered expansion.

3 There were rapid rebounds after mass extinctions when local and global diversity recovered to pre-extinction levels during relatively short spans of time. This suggests that ecospace which had been vacated as a result of an extinction event could refill faster than new ecospace. Such rapid rebounds may suggest a logistic/equilibrium model of diversification (Sepkoski 1996). Arguably, they could also be understood in a world of unfettered expansion, especially since most rebounds (mid-Cambrian, post-Ordovician, post-Permian, post-Triassic, post-Cretaceous) were associated with overall rises in global diversity to levels higher than prior to the extinction.

4 Late phases of diversification are associated with an increase in competition, evidenced by declining rates of origination and increasing rates of extinction. This corresponds to the slowing down of diversification rates as the logistic curve approaches the equilibrium level. The marine record generally confirms such expectations, but not entirely. For marine orders, total origination rates decline as a function of diversity, but total extinction rates do not increase as expected. A similar mismatch was discovered for families of marine animals; total origination rates of the Cambrian evolutionary fauna did not show the expected decline in the Late Cambrian, nor did total extinction rates of the Palaeozoic evolutionary fauna clearly increase through the Palaeozoic. These mismatches could indicate serious weaknesses of the equilibrium interpretation, or they could be the result of additional evolutionary factors that were overlaid on a three-phase logistic model (Sepkoski 1984).

5 The Palaeozoic plateau in marine animal diversity (Fig. 2.4.1.3a) is generally taken as strong evidence for equilibrium (Sepkoski 1984, 1996). A second view, however, is that the Palaeozoic plateau is real, but was maintained below any maximum carrying capacity by perturbations, i.e. extinction events of varying magnitude. A third view is that the plateau is an artefact of analyses carried out at high taxonomic level (Benton 1997). A comparison of plots of the diversity of marine life through time, shown at ordinal, familial, generic, and specific level (Fig. 2.4.1.5) shows how the logistic pattern appears to decay into an exponential pattern. At ordinal level, there is a single plateau, lasting for over 450 myr. At familial level, the Palaeozoic plateau lasts for over 200 myr. At generic level, the Palaeozoic plateau is present, but it is relatively lower than the familial plateau, and the post-Palaeozoic diversification of genera is more exponential in appearance. For species, there is no available empirical curve; a suggested consensus plot retains indications of a two-phase Palaeozoic

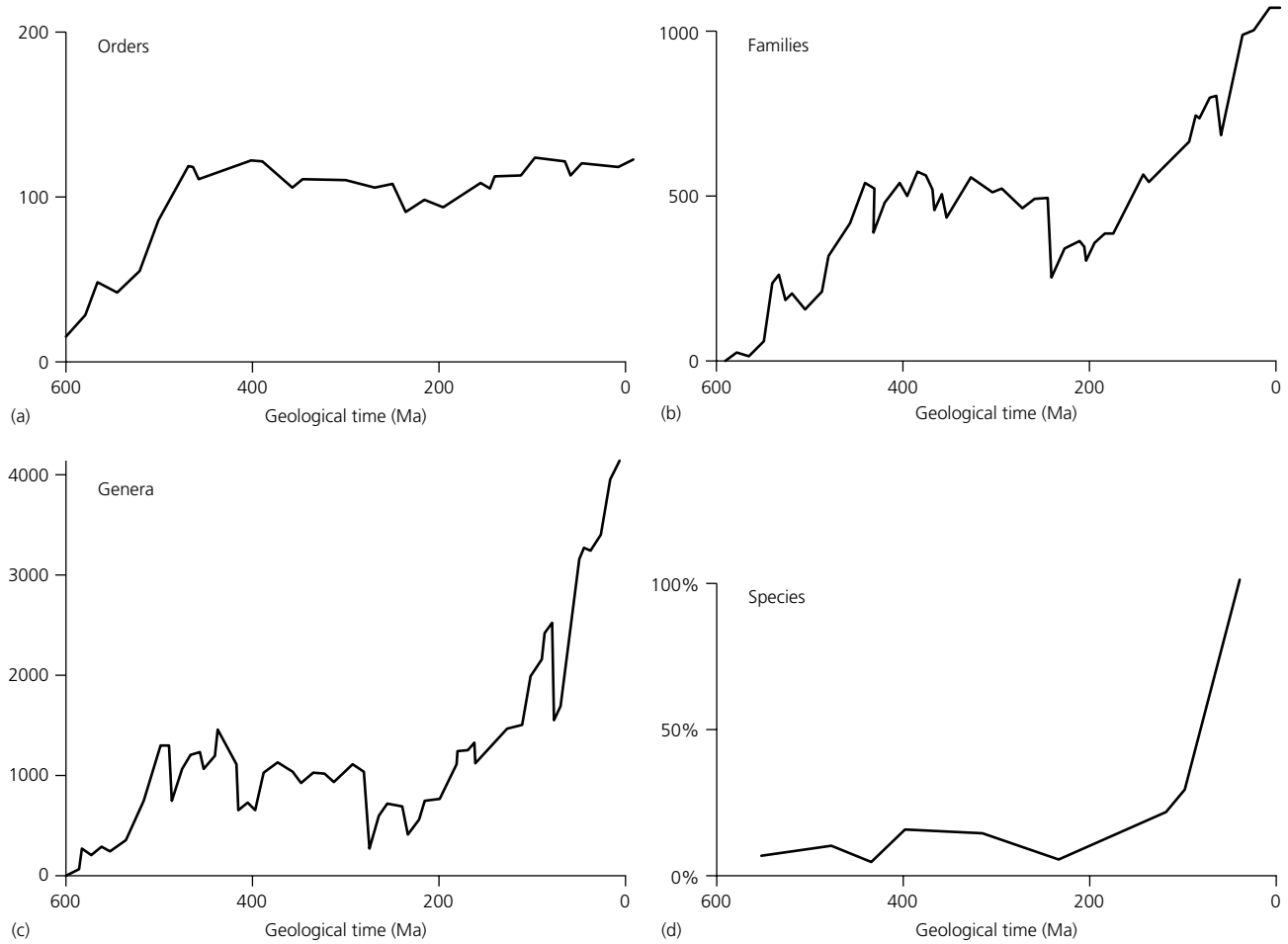

Fig. 2.4.1.5 Patterns of diversification of well-skeletonized marine animals, counted as: (a) orders; (b) families; (c) genera; and (d) species. The ordinal, familial, and generic counts are based on empirical data, while the species curve is based on real counts and on simulations, and the curve is plotted as percentages of the modern total, set at 100%. (Based on Benton 1997.)

diversification pattern, but the pattern of diversification on the whole is exponential.

Conclusion

Charles Darwin was impressed by the seemingly endless diversity of life, and studies of biodiversity are just as important now as they were in his day. It is hard to establish the current diversity of life, and even harder to estimate past diversities and how life has diversified since its origin. There are two very different models for the diversification of life: equilibrium and expansion. The equilibrium model assumes that specific major ecological realms can accommodate only certain numbers of species, and that when the carrying capacity is reached, net diversification ceases. The expansion model makes no such assumption, and allows for continuing, if episodic, diversification with no ultimate limit in sight.

Palaeobiologists have debated, and continue to debate, which model is correct. Perhaps all of life has diversified according to either an equilibrium or an expansion model. Or perhaps different sectors of life diversified in different ways. Evolution in the sea may have resulted in a greater level of stability, and patterns of increase may have generally been logistic, while life on land may have diversified exponentially since the first plants and arthropods crept cautiously out of the water. The implications of the equilibrium and expansion models are profoundly different, not merely for palaeobiologists, but for everyone concerned about the present and future state of global biodiversity.

References

Benton, M.J. (1985) Mass extinction among non-marine tetrapods. *Nature* **316**, 811–814.

Benton, M.J. (1987) Progress and competition in macroevolution. *Biological Reviews* **62**, 305–338.
Benton, M.J. (1993) *The Fossil Record 2*. Chapman and Hall, London.
Benton, M.J. (1995) Diversification and extinction in the history of life. *Science* **268**, 52–58.
Benton, M.J. (1997) Models for the diversification of life. *Trends in Ecology and Evolution* **12**, 490–495.
Erwin, T.L. (1982) Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopterists' Bulletin* **36**, 74–82.
Hewzulla, D., Boulter, M.C., Benton, M.J. and Halley, J.M. (1999) Evolutionary patterns from mass originations and mass extinctions. *Philosophical Transactions of the Royal Society of London B* **354**, 463–469.
Labandeira, C.C. and Sepkoski, J.J. Jr (1993) Insect diversity in the fossil record. *Science* **261**, 310–315.
May, R.M. (1990) How many species? *Philosophical Transactions of the Royal Society of London B* **330**, 292–304.
May, R.M. (1994) Conceptual aspects of the quantification of the extent of biological diversity. *Philosophical Transactions of the Royal Society of London B* **345**, 13–20.
Niklas, K.J., Tiffney, B.H. and Knoll, A.H. (1985) Patterns in vascular land plant diversification: a factor analysis at the species level. In: J.W. Valentine, ed. *Phanerozoic diversity patterns*, pp. 97–128. Princeton University Press, Princeton, New Jersey.
Sepkoski, J.J. Jr (1984) A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. *Paleobiology* **7**, 36–53.
Sepkoski, J.J. Jr (1992) Phylogenetic and ecologic patterns in the Phanerozoic history of marine biodiversity. In: N. Eldredge, ed. *Systematics, ecology, and the biodiversity crises*, pp. 77–100. Columbia University Press, New York.
Sepkoski, J.J. Jr (1996) Competition in macroevolution: the double wedge revisited. In: D. Jablonski, D.H. Erwin and J.H. Lipps, eds. *Evolutionary paleobiology*, pp. 211–255. University of Chicago Press, Chicago.
Valentine, J.W., Tiffney, B.H. and Sepkoski, J.J. Jr (1991) Evolutionary dynamics of plants and animals. *Palaios* **6**, 81–88.
Wilson, E.O. (1992) *The diversity of life*. Harvard University Press, Cambridge, Massachusetts.

2.4.2 Late Ordovician Extinction

P.J. BRENCHLEY

Introduction

About 22% of all families became extinct in the Late Ordovician, which makes this one of the largest episodes of mass extinction. The extinction qualifies as a mass extinction in terms of its magnitude, its global nature, the taxonomic breadth of the extinction, the breadth of the ecological disruption, and the short time span over which the extinction occurred.

Timing of extinction

The extinction occurred in two separate phases, one coinciding with the base of the Hirnantian Stage, and the second in the middle part of the Hirnantian (Fig. 2.4.2.1) (Brenchley *et al.* 1995). The base of the Hirnantian approximates closely to the base of the *Normalograptus*

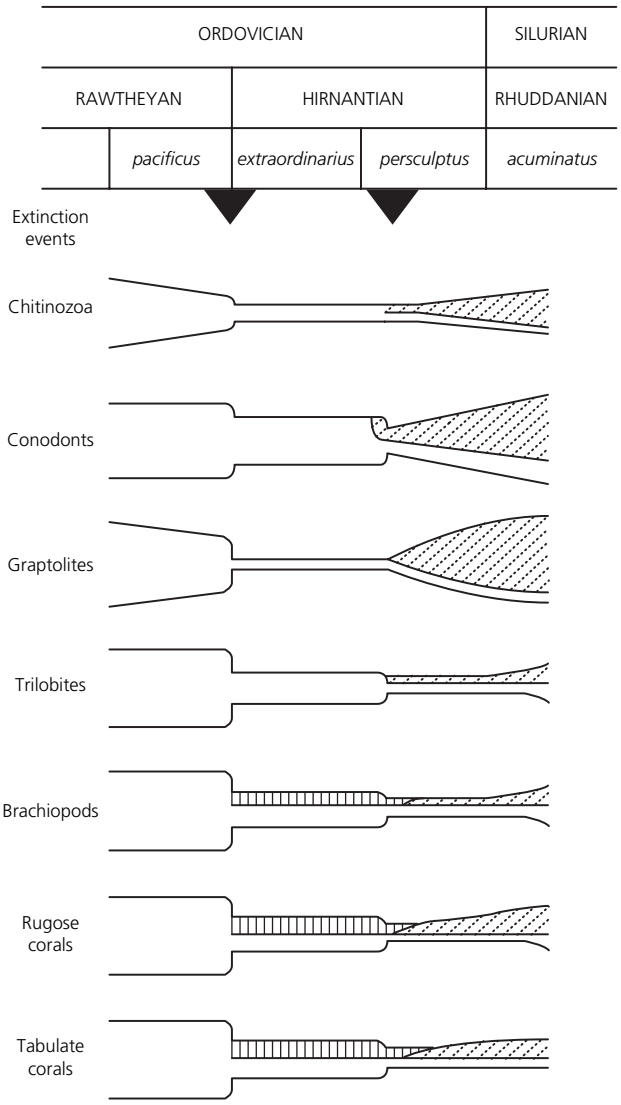

Fig. 2.4.2.1 Schematic representation of the estimated changes in diversity across the two phases of the Late Ordovician mass extinction. Biotas of pre-extinction origin are unshaded; biotas diversifying in the Hirnantian, but mainly confined to that stage, are shown with vertical shading; early representatives of the new faunas typical of the Early Silurian radiation are shown with stippled ornament.

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Benton, M.J. (1987) Progress and competition in macroevolution. *Biological Reviews* **62**, 305–338.
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Benton, M.J. (1995) Diversification and extinction in the history of life. *Science* **268**, 52–58.
Benton, M.J. (1997) Models for the diversification of life. *Trends in Ecology and Evolution* **12**, 490–495.
Erwin, T.L. (1982) Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopterists' Bulletin* **36**, 74–82.
Hewzulla, D., Boulter, M.C., Benton, M.J. and Halley, J.M. (1999) Evolutionary patterns from mass originations and mass extinctions. *Philosophical Transactions of the Royal Society of London B* **354**, 463–469.
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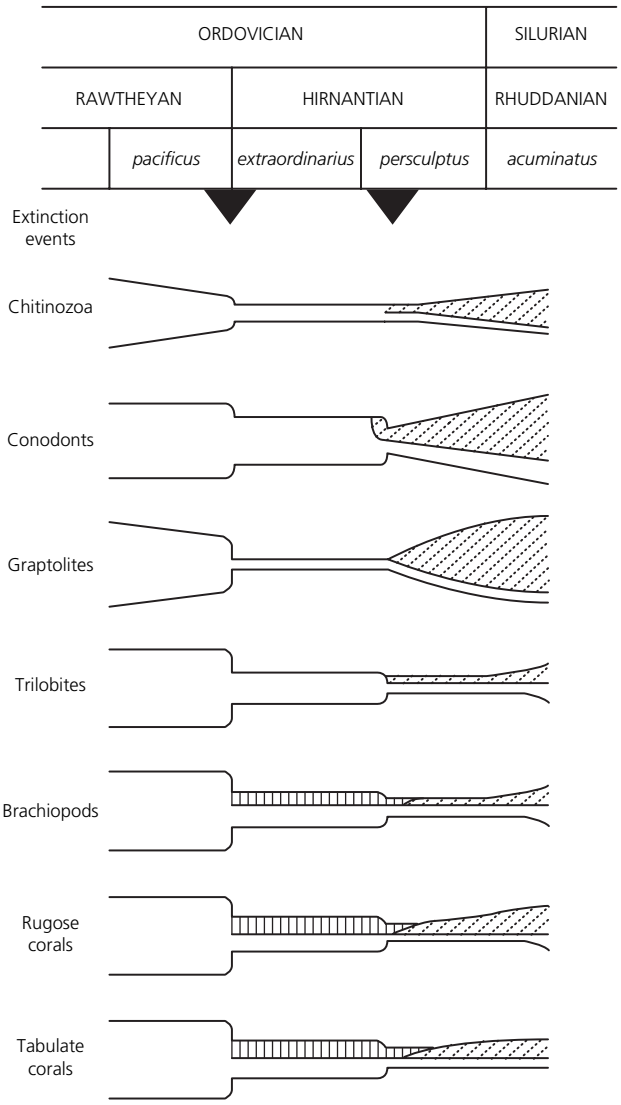

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extraordinarius graptolite Biozone, and the middle Hirnantian event to the lower part of the *Normalograptus persculptus* Biozone. The events are estimated to be about 0.5–2 million years apart.

Extinction patterns

Nearly all major benthic and planktic groups appear to have been reduced substantially by one or both phases of extinction (Fig. 2.4.2.1) (Hallam and Wignall 1997).

Chitinozoans and acritarchs

Both chitinozoans and acritarchs appear to have declined in diversity through the Rawtheyan and reached low levels in the lower Hirnantian. However, it is difficult to determine whether there was a particularly sharp drop in diversity during either of the main phases of extinction.

Graptolites

The diversity of graptolites declined through the *Paraorthograptus pacificus* Subzone (Fig. 2.4.2.1), but suffered a sharp decrease in the first phase of extinction, when most typical Late Ordovician lineages disappeared and possibly less than 10 species survived.

Trilobites

The main phase of extinction of genera and species occurred abruptly in the first extinction event, when it is estimated that as few as 50% of genera survived. Consequently, the diversity of trilobites in Hirnantian assemblages is low. However, several long-established trilobite clades persisted through the lower Hirnantian, only to disappear in the second phase of extinction.

Brachiopods

Thirteen of 27 families (and, according to one estimate, 150 of 180 genera) became extinct in the Late Ordovician. The first phase of extinction was abrupt; 60% of genera were lost. The second phase also appears to have been sharp, though some taxa initially survived the extinction, only to become extinct soon after.

Corals

Solitary rugose corals and tabulate corals suffered substantial extinction in the first event, but a new fauna became established in tropical regions during the lower Hirnantian. This, however, mainly disappeared during the second phase of extinction, so that a pre-extinction diversity of 130 genera was reduced to 40.

The broader pattern

Crinoids and cystoids suffered a substantial Late Ordovician decline in diversity, probably coinciding with the base of the Hirnantian. Amongst molluscs, the nautiloids (125 genera down to 25), gastropods (88 down to 55), and bivalves (84 down to 32) show a similar decline. In the case of the nautiloids, the state of their taxonomy may influence this estimate; in other groups the timing of extinction is not always well established.

The first phase of extinction was abrupt for such diverse benthic groups as brachiopods, trilobites, and corals. The decline in diversity of graptolites, and possibly acritarchs and chitinozoans, accelerated sharply. The residual benthic associations, which persisted through the lower Hirnantian, were dominated by the exceptionally cosmopolitan *Hirnantia* fauna. This ranged from high latitudes to the tropics (Rong and Harper 1988), though a different brachiopod fauna (the Edgewood fauna) was present in most tropical carbonate environments. The *Hirnantia* fauna may be regarded as a eurythermal, cool-adapted, opportunistic fauna, which took advantage of the preceding extinction. The second phase of extinction eliminated many elements of the *Hirnantia* fauna and much of the coral fauna that had appeared during the lower Hirnantian. It also eliminated additional elements of groups affected by the first phase of extinction, and it apparently took a heavy toll of the conodonts.

Ecological changes

The prevalent effect of the extinction was to eliminate some species from most communities, though few communities completely disappeared. The extinction amongst brachiopods seems to have been most severe in relatively shallow water and in the low diversity deep-water *Foliomena* community. The well-established shelf trilobite assemblages were greatly reduced in the first phase of extinction and most of the mesopelagic and atheloptic trilobites (forms with reduced or no eyes) amongst deep-water assemblages disappeared. More generally, cosmopolitan species survived better than endemic ones. In spite of the large extinction of species, genera, and families, the structure of Silurian communities was not greatly different from that in the Ordovician and there was relatively little ecological innovation in the filling of vacant niches.

Environmental changes

The two phases of Late Ordovician extinction were associated with the growth and decay of a large Gondwanan ice cap and related environmental changes. The main development of the ice cap in North Africa has been

dated as lower Hirnantian by graptolites and more especially by chitinozoans collected from below the glacial deposits, from sediments interbedded with glacial deposits, and from those directly overlying the glacial sequence. Associated with the growth of the ice cap was a glacio-eustatic fall in sea level of 50–100 m; this is reflected globally by lower Hirnantian regressive sequences and by one or more pronounced erosional sequence boundaries in many sections (Fig. 2.4.2.2). The ensuing rise of sea level, coeval with the second phase of extinction, produced a transgressive sequence that initially filled incised valleys and then formed a blanket of anaerobic or dysaerobic dark grey shales over many regions.

A positive $\delta^{18}O_{carb}$ excursion of ≈4‰ (Fig. 2.4.2.2) indicates the growth of major ice caps and possibly a fall in seawater temperature by as much as 8°C, even in the tropics. A contemporaneous global positive excursion in $\delta^{13}C_{carb}$ of ≈7‰ indicates a major change in carbon cycling, as would accompany increased productivity in the oceans and increased burial of carbon or sequestration in deep water (Brenchley *et al.* 1994).

The rapid global cooling and growth of ice caps marked a change from long-established greenhouse conditions to ice-house climates. Such changes are likely to have disrupted the warm saline bottom waters in the ocean by the creation of a new regime of vigorous thermohaline circulation. Associated upwelling might have lifted the thermocline and oxygen minimum zone and advected toxic waters into the mixed layer containing planktic and nektonic habitats (Berry *et al.* 1995).

Causes of extinction

The close correlation between the two phases of extinction and the growth and decay of the Gondwanan ice caps suggests that climatic or related environmental changes caused the extinctions. The first phase was apparently coeval with the start of global cooling, the initiation of falling sea level, and a change in carbon cycling in the oceans. Even though the temperature change still might have been modest at the time of extinction, the unusually rapid decrease in seawater temperature which affected even tropical waters may have had a profound affect on specialized oligotrophic shelf biotas accustomed to a greenhouse climate. Extinction amongst the zooplankton (graptolites) and nekton (some trilobites) that lived just outside the shelf margin may have resulted from the changes to oceanic circulation and upwelling that advected toxic and possibly over-nutrient-rich waters up into the surface layers of the oceans (Berry *et al.* 1995). A fall in sea level seems an unlikely cause, because at the time of the first phase of extinction, the fall was relatively modest and is unlikely to have modified shelf area or habitat diversity sufficiently to have caused major ecological disruption (Brenchley *et al.* 1995). However, it is possible that there was extinction amongst the benthic faunas of shallow carbonate platforms as sea level fell and wide areas were exposed in the period between the two main phases of extinction.

The second main phase of extinction coincided with the decay of the Gondwanan ice caps, climatic warming, rapid sea-level rise, and oceanic changes that brought

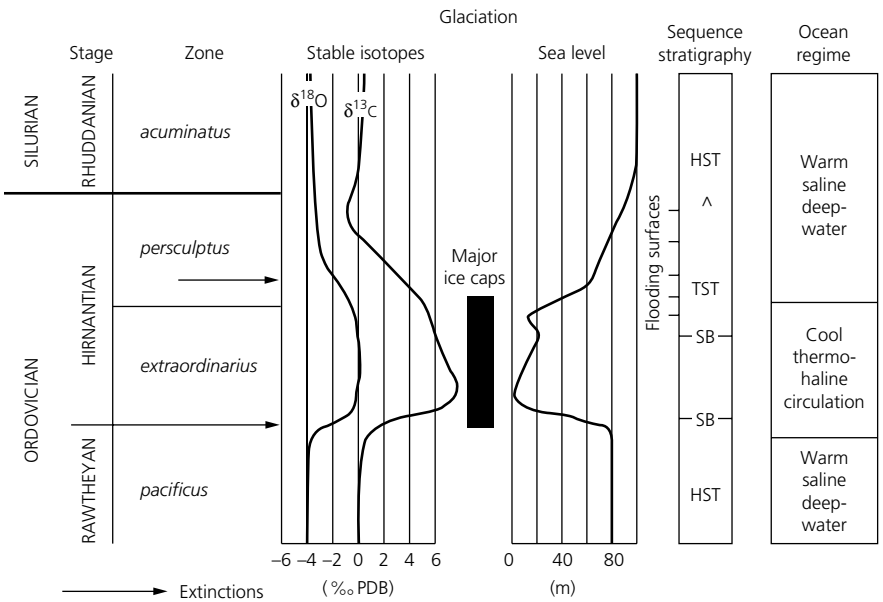

Fig. 2.4.2.2 Late Ordovician environmental changes and their relationship to the two main phases of the mass extinction. HST, highstand systems tract; SB, sequence boundary; TST, transgressive systems tract.

about widespread anoxia in both shallow and deep waters. Biotas that had survived the environmental changes associated with climatic cooling were then faced with climatic warming. It is difficult to isolate which of the several coeval environmental changes may have been particularly lethal. However, the rapid and relatively deep flooding of shelf areas, coupled with widespread anoxia, might explain the relative rarity of shallow marine faunas of Early Silurian age and possibly the extinction of conodonts too. Rapid warming may have played a part by affecting cool-adapted species, particularly some members of the *Hirnantia* fauna.

In summary, the Late Ordovician extinction appears to have resulted from linked major climatic, oceanographic, and sea-level changes, associated with the rapid growth and decay of the Gondwanan ice cap. The scale and particularly the rapidity of the environmental changes are likely to have been crucial factors in precipitating the two episodes of biotic mortality that together constitute this mass extinction.

References

Berry, W.B.N., Quinby-Hunt, M.S. and Wilde, P. (1995) Impact of Late Ordovician glaciation and deglaciation on marine life. In: S.M. Stanley *et al.*, eds. *Effects of past global change on marine life*, pp. 34–46. Studies in Geophysics, National Academy Press, Washington.

Brenchley, P.J., Marshall, J.D., Carden, G.A.F., Robertson, D.B.R., Long, D.G.F., Meidla, T., Hints, L. and Anderson, T. (1994) Bathymetric and isotopic evidence for a short-lived Late Ordovician glaciation in a greenhouse period. *Geology* **22**, 295–298.

Brenchley, P.J., Carden, G.A.F. and Marshall, J.D. (1995) Environmental changes associated with the 'first strike' of the late Ordovician mass extinction. *Modern Geology* **20**, 69–82.

Hallam, A. and Wignall, P.B. (1997) *Mass extinctions and their aftermath*. Oxford University Press, Oxford.

Rong Jia-yu and Harper, D.A.T. (1988) A global synthesis of the latest Ordovician Hirnantian fauna. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **79**, 383–402.

2.4.3 Late Devonian Extinction

G.R. McGHEE Jr

Introduction

The Late Devonian extinction is one of the 'Big Five' mass extinctions that have occurred in the past 600 myr of metazoan evolution (the other four being end-Ordovician, end-Permian, end-Triassic, and end-Cretaceous). The Late Devonian extinction is unusual in that it occurred within the last epoch of the Devonian Period, at the boundary between the Frasnian and Famennian stages, and not at the end of the geological period, as did the other four mass extinctions. At least 70% of all marine species perished in the Late Devonian extinction, and some estimates suggest that the species kill may have been as high as 82% (McGhee 1996).

Timing of extinction

The Late Devonian extinction was not a single event, but occurred in five main pulses spread over 1.0–1.5 myr in the latest Frasnian and earliest Famennian (365.0–363.5 Ma; Fig. 2.4.3.1). The first of the extinction pulses is termed the Lower Kellwasser Event (Table 2.4.3.1), named after the Kellwasser Limestone units in Germany (Walliser 1996). It was followed some 500–800 kyr later by three extinction pulses in the latest Frasnian (Fig. 2.4.3.1), which are termed here the Upper Kellwasser Events (Table 2.4.3.1): one at the base of the Upper Kellwasser Limestone unit, another within the unit, and a third at the top. The sum of these three pulses was much more severe than the Lower Kellwasser event, and within the Upper Kellwasser interval the last pulse was much more severe than the first two (McGhee 1996). All three extinction pulses are estimated to have occurred in the last 100–300 kyr of the Frasnian (Walliser 1996). A final extinction pulse occurred in the earliest Famennian (Fig. 2.4.3.1) and is termed here the Homoctenid Event (Table 2.4.3.1). The homoctenids are members of the Cricoconarida: tiny, cone-shaped organisms whose mode of life was similar to modern planktic gastropods like pteropods. The cricoconarids were a major element of the Devonian zooplankton and were totally eliminated in the Late Devonian mass extinction. Huge numbers of cricoconarids perished in the latest Frasnian, and only the tiny homoctenids survived into the Famennian before suffering extinction themselves.

Extinction patterns

The most spectacular victims of the Late Devonian mass extinction were the reefs. Devonian reef ecosystems were the most geographically extensive that have ever occurred in Earth history, almost 10 times the areal extent of reefs in modern oceans. Tropical reef and peri-reefal ecosystems were destroyed in the Late Devonian extinction, shrinking by a factor of 5000 in areal extent from the Frasnian Stage to the Famennian. Tabulate corals and stromatoporoids (extinct sponges), major elements of the reef biota, did not recover their diversity losses for the remainder of their evolutionary history, and reef ecosys-

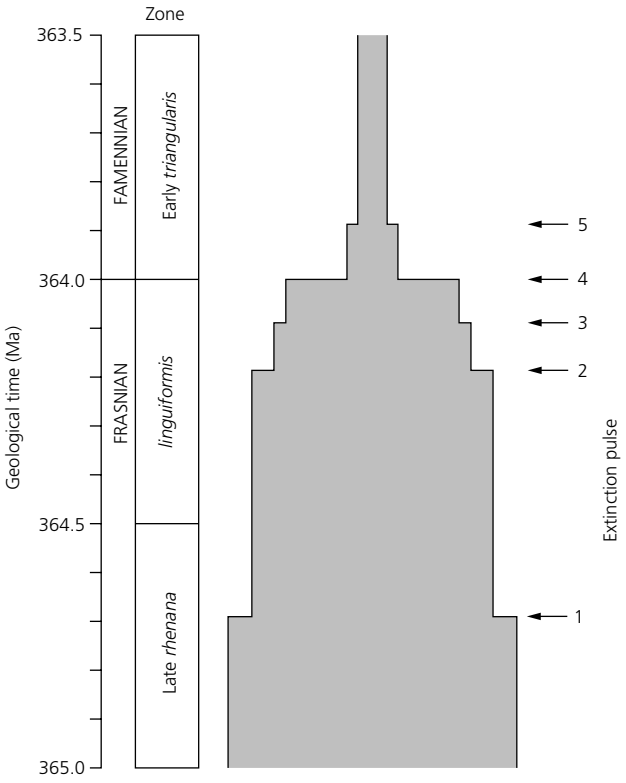

Fig. 2.4.3.1 Temporal pattern of biotic diversity loss in the Late Devonian mass extinction. Five extinction pulses (numbered in right margin of figure) occurred during the latest Frasnian and earliest Famennian (365.0–363.5 Ma).

tems as a whole did not recover for the remainder of the Palaeozoic. Many other inhabitants of the marine benthos were severely affected by the extinction. The Devonian was the 'Golden Age' of the brachiopods, which were the dominant elements of the benthic shellfish in Palaeozoic seas, an ecological position held by the molluscs today. The brachiopods lost more than 75% of their genera in the extinction, and the biconvex brachiopods in particular did not recover for the remainder of their evolutionary history.

The extinction was not confined to benthic organisms in the Earth's oceans: the plankton (passive floaters) and nekton (active swimmers) also suffered severe diversity losses. As mentioned above, the cricoconarids became extinct in the Late Devonian, representing an extinction at the class-level of the taxonomic hierarchy and the loss of a major element of Devonian zooplankton. In addition to these tiny animals, an estimated 90% of the preservable phytoplankton in the world's oceans was also lost in the Late Devonian.

In the nekton, the pelagic-carnivore ecological niche was virtually vacated in the Late Devonian extinction. Only eight genera of ammonoids survived the late Frasnian Stage. Over half the species of placoderm fish died out, and the survivors were mostly freshwater species. Fully one-third of the surviving placoderm fish families left the marine environment entirely as a consequence of the ecological selectivity of the Late Devonian extinction. Among the pelagic conodonts (tiny eel-like swimmers of chordate affinity), only three species survived the Late Devonian extinction.

On land, major losses in terrestrial plant diversity occurred. The early amphibians vanish from the rock record, and only much later in the Famennian did they recover sufficient population sizes to reappear.

Ecological signature

Extensive analysis of the pattern of extinction and survival of species during the Late Devonian mass extinction has revealed five non-random ecological signals in the data: (1) the biosphere of the entire planet was affected, both marine and terrestrial; (2) life in equatorial and low latitude regions was most severely affected, and diversity loss was not as great in higher latitude regions; (3) latitudinal compression of geographical range occurred in surviving low latitude faunas (i.e. faunas with ranges that extended from the equator into mid-latitude regions in the Frasnian were restricted to equatorial regions in the Famennian); (4) life in shallow-water marine habitats was most severely affected, and diversity loss was not as great in deeper water habitats; and (5) clades with representatives in both marine and freshwater habitats (e.g. fish) experienced severe diversity losses in their marine species, but less reduction in diversity in terrestrial freshwater species (McGhee 1996).

Causes of extinction

The two most probable causes that have been proposed for the Late Devonian extinction are global oceanic anoxia and global cooling (McGhee 1996; Hallam and Wignall 1997). It is clear that much of the oceanic deep-water region was anoxic during the Late Devonian, as is evidenced by the global distribution of black shales, including the Kellwasser bituminous limestone units themselves. The lethal spread of anoxic waters into shallow-water regions would have produced many of the ecological signatures evident in the Late Devonian extinction, such as the differential survival of deep-water species (tolerant of low oxygen) and freshwater species (which never encountered the anoxic marine waters). It may also explain the observed differential survival of high latitude marine species over low latitude, as the spread of anoxic oceanic waters would have been more extensive in warm water regions than cold.

The oceanic anoxia model cannot explain the fact that terrestrial as well as marine ecosystems were affected

Table 2.4.3.1 Timing of extinction events and possible bolide impacts during the last 4 million years of the Frasnian Stage (FRA), and the first 2.5 million years of the Famennian Stage (FAM), within the Late Devonian Epoch. Ages are given in millions of years before the present, modified from the geological time scales given by McGhee (1996) and Gradstein and Ogg (1996).

Stage	Zone	Age	Extinction event	Impact evidence
	Late *crepida*	361.5		
	Middle *crepida*	362.0		
	Early *crepida*	362.5		China, Australia
	Late *triangularis*	363.0		
	Middle *triangularis*	363.5		
FAM	Early *triangularis*	364.0	Homoctenid Event	Belgium, China
FRA	*linguiformis*	364.5	Three Upper Kellwasser Events	China
	Late *rhenana*	365.0	Lower Kellwasser Event	Australia
	Early *rhenana*	365.5		
	jamieae	366.0		
	Late *hassi*	366.5		
	Early *hassi*	367.0		
	punctata	367.5		USA
	transitans	368.0		

during the Late Devonian mass extinction, and it cannot account for the observed latitudinal compression of the surviving low latitude faunas in the marine realm. Neither does it explain satisfactorily the observed mass killing of the plankton in shallow marine waters, as the upper 50–100 m of oceanic waters are generally well oxygenated by wind and wave action, regardless of the degree of anoxia present in deeper waters. A modified version of the oceanic anoxia model, the oceanic overturn model, has been proposed to solve this latter problem. In an overturn event, poisonous bottom waters would be brought all the way up to the surface and thus could indeed kill the plankton. However, triggering a global overturn of the world's oceans is problematic and, in order to account for the temporal signature of the mass extinction, such an overturn must have occurred several times. Interestingly, models of the density structure of the world's oceans suggest that a global overturn of the oceanic water column could perhaps be triggered by global cooling (McGhee 1996).

Lethal global cooling would produce all of the ecological signals observed in the Late Devonian extinction: the differential survival of deep-water marine species, high latitude marine species, and freshwater terrestrial species (all cold tolerant), and the latitudinal compression of surviving low latitude faunas (cold intolerant). In contrast to the oceanic anoxia model, the global cooling model easily explains the destruction of the surface-water marine plankton and also accounts for the extinctions of terrestrial animal and plant species far from the oceans. The temporal signature of the Late Devonian extinction—pulses of extinction on multiples of 100 kyr scales occurring over a 1–2 myr interval (Fig. 2.4.3.1)—is very similar to that seen in the glacial cycles of the Late Pliocene and Pleistocene. Unfortunately for the global cooling model, all attempts to produce evidence for glaciation in the late Frasnian and early Famennian have failed (McGhee 1996; Hallam and Wignall 1997).

Multiple impacts hypothesis

Multiple impacts of asteroids or comets on the Earth have been proposed as an alternative to glaciation as a mechanism for producing pulses of global cooling (McGhee 1996). The Late Devonian does seem to have been a time of increased impact frequency, in that from 6 to 10 known terrestrial impact craters are currently thought to be of Late Devonian age. Two of these, the Siljan crater in Sweden and the Charlevoix crater in Canada, are definitely of Late Devonian age and are quite large (52 km and 46 km in diameter, respectively).

The best dated evidence (Table 2.4.3.1) indicates that bolide impacts on the Earth occurred in the *punctata* Zone of the Frasnian in Nevada, USA, in the Famennian early *triangularis* Zone in Belgium, and in the early *crepida* Zone in China (McGhee 1996). There is a host of evidence, including impact-shocked minerals and an iridium anomaly, for the *punctata* impact. Evidence for the early *triangularis* and early *crepida* impacts comes from microtektites (impact melt glasses) found in sediments of these ages. However, only the early *triangularis* impact corresponds to any of the Late Devonian extinction pulses (Table 2.4.3.1).

More controversial evidence has been offered for possible impact events in the latest Frasnian and early Famennian from China and Australia, as well as for the early *crepida* impact from Australia (Table 2.4.3.1). Iridium anomalies have been reported from the late *rhenana* Zone and the early *crepida* Zone in Australia (McGhee 1996). However, the iridium in sediments of these ages occurs in microstromatolites produced by the

cyanobacterium *Frutexites*, and has clearly been microbially concentrated. Thus it is uncertain whether the iridium 'anomaly' is due to biological concentration, to fallout produced by an asteroid impact, or both. Three anomalous nickel concentration horizons have been reported from the *linguiformis* Zone, and two from the early *triangularis* Zone, in China (Bai *et al.* 1994). Microspherules, possibly the remains of microtektites, have also been reported from these sediments (Bai *et al.* 1994). Although these additional proposals for impact events do occur during the critical interval of the Late Devonian mass extinction (Table 2.4.3.1), they remain highly controversial.

Another difficulty for the multiple impacts hypothesis arises from the fact that the Earth is known to have encountered comet showers in the past that did not trigger major extinctions. The Earth was impacted by at least three bolides during the Late Eocene (35 Ma), and two of these were quite large: the Chesapeake Bay impact (Virginia, USA) left a crater some 85 km in diameter, and the Popigai impact (Siberia, Russia) produced a 100-km crater. Yet the fossil record for this same period of geological time does not record major disruptions of the planet's biosphere.

Summary

It is possible that no single cause was responsible for the Late Devonian crisis, and that the mass extinction was triggered by a combination of factors. For example, the great Devonian reefs were most severely stricken in the Lower Kellwasser Event, and both that event and the first of the Upper Kellwasser Events (Table 2.4.3.1) primarily killed benthic marine organisms. Thus it is possible that the first two events in the Late Devonian extinction might have been triggered by the spread of anoxic bottom waters.

In contrast, the subsequent three extinction events (the second and third Upper Kellwasser Events, and the Homoctenid Event; Table 2.4.3.1) devastated the surface-water marine plankton. These plankton extinctions, in combination with the extinctions of plants and animals that occurred on land, could not have been triggered by marine anoxia. Three episodic events of lethal global cooling best fit the ecological pattern exhibited by these extinctions. The triggering mechanism for these pulses of global cooling is unknown, but may have been multiple impacts of asteroids or comets with the Earth during the latest Frasnian and earliest Famennian.

References

Bai, S.L., Bai, Z.Q., Ma, X.P., Wang, D.R. and Sun, Y.L. (1994) *Devonian events and biostratigraphy of South China*. Peking University Press, Beijing.

Gradstein, F.M. and Ogg, J. (1996) A Phanerozoic time scale. *Episodes* **19**, 3–5.

Hallam, A. and Wignall, P.B. (1997) *Mass extinctions and their aftermath*. Oxford University Press, Oxford.

McGhee, G.R. Jr (1996) *The Late Devonian mass extinction*. Columbia University Press, New York.

Walliser, O.H. (1996) Global events in the Devonian and Carboniferous. In: O.H. Walliser, ed. *Global events and event stratigraphy*, pp. 225–250. Springer-Verlag, Berlin.

2.4.4 End-Permian Extinction

P.B. WIGNALL

Introduction

The mass extinction at the end of the Permian was by far the most severe crisis in the history of life: more than 60% of animal families, both marine and terrestrial, disappeared (Benton 1995). In the oceans the crisis removed the diverse epifaunal communities characteristic of late Palaeozoic sea floors and left just one dominated by a few species of bivalve (e.g. *Claraia*). Sponge reefs were well developed in latest Permian equatorial settings of the Tethyan Ocean, notably in South China, but they also disappeared at the end of the Permian. Reefs do not reappear in the fossil record until the Middle Triassic, 10 myr later.

Timing of extinction

Although the extinction was traditionally viewed as a protracted crisis, perhaps spread over the last 8–10 myr of Permian times, recent work indicates a more complicated but dramatic picture (Fig. 2.4.4.1) (Hallam and Wignall 1997). Two distinct extinction events have been identified, separated by a phase of recovery and radiation. The first extinction, at the end of the Middle Permian (Guadalupian Stage), affected low latitude marine faunas, particularly the fusulinids (a group of large, multichambered foraminifera) and echinoderms (principally the crinoids, echinoids, and probably all blastoids). The second more severe event, near the close of the Permian, affected a broader spectrum of faunas from all latitudes and appears to have been of short duration (<1 myr).

Extinction patterns

The end-Permian crisis marked a major bottleneck in the evolution of the majority of marine invertebrate groups.

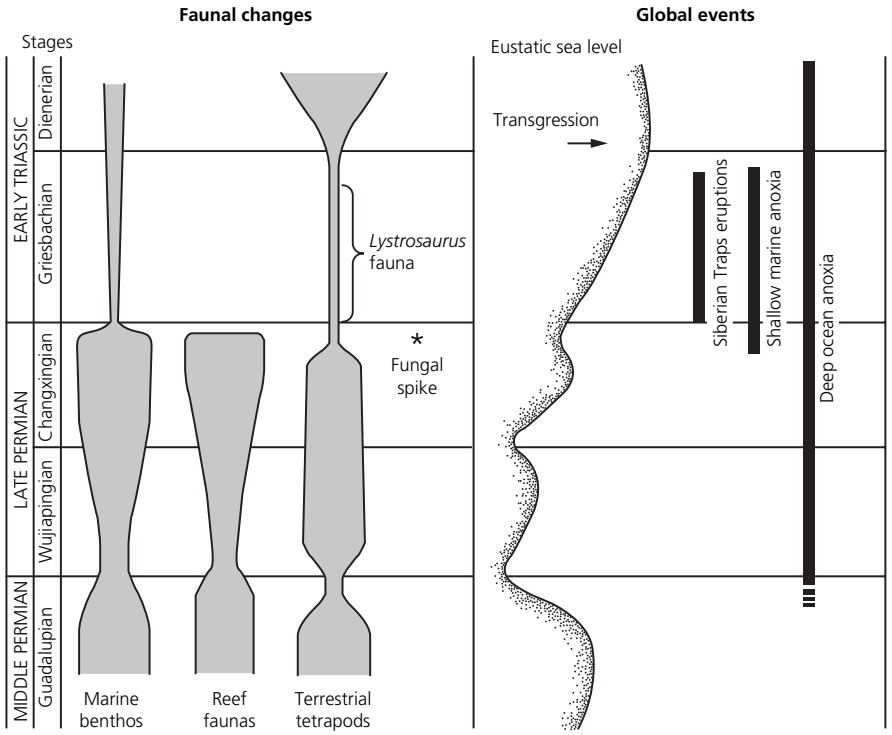

Fig. 2.4.4.1 Summary of faunal changes and global events at the time of the end-Permian mass extinction. Note that the main phase of extinction, late in the Changxingian Stage, coincides with a proliferation of fungal spores in the palynological record, the initial phases of a sea-level rise, the expansion of anoxic conditions into shallow shelf locations, and possibly the onset of Siberian Traps eruptions (although this may slightly postdate the extinction).

The brachiopods and crinoids, both highly diverse Permian groups, never again achieved either their former abundance or diversity while, in many other groups, previously minor clades rose to importance when dominant lineages became extinct. This is particularly apparent for the bryozoans, echinoids, bivalves, and ammonoids. Other groups entirely disappeared (e.g. trilobites, and rugose and tabulate corals). Overall, the most significant long-term effect of the crisis was the replacement of sea-floor communities dominated by large, sessile, epifaunal taxa (e.g. crinoids, bryozoans, rugose corals, and brachiopods) with ones dominated by infaunal and vagile epifaunal molluscs (bivalves and gastropods). A further intriguing aspect of the benthic extinctions was the importance of the Lazarus effect. This denotes the tendency for some taxa to disappear from the fossil record and reappear (as if 'born again' like the biblical namesake) a considerable time later. Examples of Lazarus taxa during the end-Permian extinction are known from the gastropods, brachiopods, and holothurians; many of these taxa do not reappear in the fossil record until the Middle or even Late Triassic. During their disappearance phase Lazarus taxa may have migrated to some (unknown) refuge or alternatively they could have become very rare and thus unlikely to be found as fossils.

Within the water column the crisis appears to have been selective and the Lazarus effect was unimportant. The various groups of fish and conodonts survived the crisis virtually unscathed, whereas at the base of the food chain the radiolarians underwent near-total extinction. This important group of heterotrophic microplankton is unknown from Lower Triassic rocks and its demise coincides with carbon isotopic evidence for a collapse of primary productivity in latest Permian oceans.

On land a double extinction is also evident, but the second event appears to have been especially severe (Fig. 2.4.4.1). A diverse range of tetrapods was eliminated, including the pareiasaurs (the dominant large herbivores), the large carnivorous gorgonopsids, and the small omnivorous millerettids. Only the small carnivorous therocephalians maintained a reasonable diversity during the crisis. In the immediate aftermath of the crisis the single dicynodont genus *Lystrosaurus* became extraordinarily abundant throughout the world. Even that most resilient of groups, the insects, suffered a major crisis at this time, the only one of their history. Plants also underwent wide-ranging extinctions. Thus, the *Glossopteris* forests of high southern latitudes disappeared, whilst at equivalent northern latitudes the high-diversity *Cordaites* flora of Siberia was also eliminated. Perhaps the most intriguing facet of the floral record is

the sudden proliferation of fungal spores during the extinction crisis. This normally rare component of palynological preparations becomes exceptionally abundant in both terrestrial and marine rocks during the extinction crisis, particularly at lower latitudes.

Events during the crisis

Recent research has added considerably to the panoply of events implicated in (or at least associated with) the end-Permian extinction. One of the most significant is a consequence of improved dating of the Siberian Traps, a vast province of flood basalts. Previously thought to be of Triassic age, dating of zircons indicates that the onset of volcanic activity began at 250 Ma, close to the Permian–Triassic boundary; the main eruptive phase lasted perhaps less than 1 myr (Campbell *et al.* 1992). A high proportion of tuffs occur within the Traps, and thick tuffs are present immediately beneath the basalt flows, suggesting that the eruptions may have been unusually explosive by the standards of flood basalts, further adding to their lethal potential.

Improved dating of marine boundary sections (primarily using conodonts), combined with detailed facies analysis, has considerably changed our appreciation of oceanographic events at this time (Hallam and Wignall 1997). The presence of a widely reported end-Permian regression is no longer tenable; a minor regression occurred within the late Changxingian Stage followed by a major transgression that continued into the Triassic (Fig. 2.4.4.1). This is one of the clearest eustatic signals of the geological record and it is significant that the marine extinctions occur during this interval of sea-level rise. Anoxic facies, characterized by finely laminated sediments containing abundant, tiny crystals of pyrite, are developed within this transgressive record in a diversity of settings, from shallow, equatorial carbonate ramps to deep, clastic shelves at high latitudes. This facies change closely coincides with the demise of many Permian taxa. In deeper water sections anoxic conditions developed considerably earlier, towards the end of the Middle Permian, and persisted to the end of the Early Triassic, suggesting a 'superanoxic' oceanic event of considerable duration (Isozaki 1997). Strange carbonate precipitates are also known from the Late Permian suggesting unusual oceanic chemistry during this interval (Knoll *et al.* 1996).

Further important insights have come from new studies of soil horizons at high palaeolatitudes. In the Karoo Basin of South Africa, wet floodplain conditions of the latest Permian give way to semiarid, calcrete-forming conditions at the end of the period. Both drying-out and increased warming is evident in sections in eastern Australia and Antarctica where soils characteristic of modern latitudes 25–38° (subtropical to temperate) are developed at palaeolatitudes 70–80°S.

Causes of extinction

Perhaps more than any other mass extinction controversy, the debate on the end-Permian crisis has been revitalized in the last few years as newly collected field data have fostered the proposal of several novel kill mechanisms. Traditional scenarios such as regression and marine habitat loss are no longer tenable in the light of the observation that the marine extinctions occurred during a phase of transgression. In fact, the close correspondence between the development of anoxic conditions and the marine extinctions suggests that oxygen deficiency was the proximate cause of many losses (Hallam and Wignall 1997). Collapse of primary productivity may also have contributed to the extinction, although details of the timing of this collapse suggest that it slightly postdates the mass extinction and may therefore have been a symptom of a progressively declining marine ecosystem.

The influence of the Siberian Traps eruptions in this crisis has been hotly debated and it is currently by no means clear whether the onset of volcanic activity coincides with the extinctions or slightly postdates it (Fig. 2.4.4.1). If the eruptions were unusually explosive, then large volumes of dust and aerosols may have been injected into the stratosphere, triggering global cooling, a short sharp glaciation, and the collapse of photosynthesis in the marine and terrestrial food chains (Campbell *et al.* 1992). However, this scenario receives little support from the geological record; evidence from high latitude palaeosols and the loss of all cold-adapted floras points to a phase of severe global warming. The principal harmful agent therefore may have been the release of huge volumes of volcanic carbon dioxide, and the consequent triggering of a super-greenhouse climate. Global warming may have made large parts of the continent of Pangaea uninhabitable and severely reduced oceanic circulation. Warming of high latitude shelf seas would have drastically decreased the generation of cold, dense, deep ocean water, and the resultant stagnation would have led to oxygen deficiency.

Aftermath

The immediate legacy of the end-Permian mass extinction was to leave a world of impoverished diversity dominated by a few, globally distributed, abundant survivors, notably *Lystrosaurus* on land and *Claraia* in the oceans. The earliest Triassic also witnessed the expansion of stromatolites from intertidal sites on to shelf locations where they commonly formed small reefs. Such

occurrences are generally very rare after the Precambrian and their presence in the Early Triassic is a measure of the devastation of the marine ecosystem. In normal marine conditions intense grazing pressure (by gastropods and echinoids) inhibits the development of stromatolites but the drastic reduction in the abundance and diversity of these groups in the aftermath of the mass extinction may have allowed the stromatolites to colonize shelf areas.

Recovery rates varied widely but were highest in terrestrial ecosystems which attained much of their pre-extinction complexity within a million years or so. Recovery in shallow marine habitats, in contrast, was substantially slower and not until the Middle Triassic did any appreciable radiation begin and Lazarus taxa reappear. Such was the magnitude of the extinction that pre-extinction diversity levels in the oceans were not attained again until the Cretaceous, over 120 myr later.

References

Benton, M.J. (1995) Diversification and extinction in the history of life. *Science* **268**, 52–58.

Campbell, I.H., Czamanske, G.K., Fedorenko, V.A., Hill, R.I. and Stepanov, V. (1992) Synchronism of the Siberian Traps and the Permian–Triassic boundary. *Science* **258**, 1760–1763.

Hallam, A. and Wignall, P.B. (1997) *Mass extinctions and their aftermath*. Oxford University Press, Oxford.

Isozaki, Y. (1997) Permo-Triassic boundary superanoxia and stratified superocean: records from the lost deep sea. *Science* **276**, 235–238.

Knoll, A.H., Bambach, R.K., Canfield, D.E. and Grotzinger, J.P. (1996) Comparative Earth history and Late Permian mass extinction. *Science* **273**, 452–457.

2.4.5 Impact of K–T Boundary Events on Marine Life

R.D. NORRIS

Introduction

The Cretaceous–Tertiary transition is associated with one of the five largest mass extinctions in the Phanerozoic; 40–76% of species present in the Late Cretaceous became extinct (Jablonski 1995). The extinction was large enough to produce major changes in nutrient cycling in the biosphere and to reset the pattern of ecological incumbency and interaction in many taxa (e.g. D'Hondt *et al*. 1996; Kelley and Hansen 1996). The causes of the extinction are commonly ascribed to the ramifying effects of atmospheric dust loading caused by a meteorite strike and resulting darkness and planetary cooling, but major climatic changes near the end of the Cretaceous may also have played a role. The immediate causes of extinction for most taxa remain speculative. Recovery to pre-extinction species diversity and ecological diversity occupied much of the Paleocene and Early Eocene.

Extinction pattern

The K–T extinction was highly selective. A number of major groups were completely killed off, such as the dinosaurs, marine reptiles, and ammonites, while others, such as the deep-sea benthic foraminifera, passed through the boundary virtually unaffected. Groups that suffered from considerable, but not complete, extinction include the planktic foraminifera (≈95% extinction; 62 of 66 species), calcareous nannofossils (≈80–85% extinction; 68 of 80 species), dinoflagellates (62% extinction; 129 of 209 species), Tethyan scleractinian corals (97–98% extinction of species), North American bivalves (70–80% extinction of species), and benthic diatoms (60–90% extinction of genera). Shelf benthic foraminifera are known to have experienced relatively modest turnover (≈39% extinction of species at the El Kef K–T stratotype in Tunisia), as did planktic diatoms (≈10–50% extinction of genera) (Speijer and van der Zwaan 1996; MacLeod *et al*. 1997).

Many other fossil groups are poorly preserved or rare, making the magnitude of their extinction difficult to estimate. For example, sharks and rays lost about 43% of genera in the late Maastrichtian (corresponding to 70–80% species loss using the genus–species relationship in Jablonski 1995) but how many of these taxa died out at the boundary is unknown. In other cases, extinction estimates are strongly affected by the methodology used to calculate diversity. Extinction estimates for echinoid genera range from 70% (MacLeod *et al*. 1997) as derived from a 'taxon-counting' exercise, to ≈36% (Smith and Jeffery 1998) based on a phylogenetic analysis and elimination of paraphyletic groups.

A common theme among many marine taxa that suffered heavy extinction at the K–T boundary was the selective loss of large-size taxa. A sharp drop in body size or size of skeletal elements is observed in planktic foraminifera, calcareous nannofossils, echinoids, bivalves, gastropods, and brachiopods. In the case of planktic foraminifera, the upper size distribution was reduced from ≈600–800 μm to ≈125 μm, reflecting partly the dwarfing of surviving taxa and partly the initial small size of survivors. Danian echinoid taxa are almost always smaller than their Cretaceous sister taxa, sug-

gesting that dwarfing may have been related to nutrient stress in the aftermath of the extinction (Smith and Jeffery 1998).

Immediate aftermath of the extinction

The first distinct 'Paleocene' taxa evolved from surviving species within 1–10 kyr of the extinction. The exact timing of the initial rebound is obscured by the pervasive mixing of Cretaceous species into overlying Paleocene sediments, and low sedimentation rates, particularly in many deep sea sites. Blooms of planktic foraminifera (*Parvularugoglobigerina eugubina*) and calcareous dinoflagellates (*Thoracosphaera*) occurred in the first 40 kyr of the Paleocene and blooms of nannofossils (*Braarudosphaera, Neobiscutum*, and *Placozygus*) continued over the next 300–400 kyr through the top of Nannofossil Zone NP1 (MacLeod *et al.* 1997). Bizarre morphologies are present in populations of the planktic foraminifer *P. eugubina*, which may indicate either a high mutation rate or weakened selection in the first 10–40 kyr of the Paleocene.

Carbon isotope gradients between surface waters and the deep ocean became reduced or even inverted for at least 500 kyr after the end of the Cretaceous, and remained low for more than 2 myr (D'Hondt *et al.* 1996). The reduced $\delta^{13}C$ gradient may reflect a weakened mechanism of exporting organic matter from the surface into the deep ocean, perhaps due to the extinction of large grazing zooplankton such as copepods and salps. A dramatic reduction of surface ocean productivity is also reflected in records of barium concentration in sediments and a ≈50% reduction in carbonate accumulation rates, which remained depressed for at least 500 kyr (D'Hondt *et al.* 1996). Barium concentrations rose abruptly about 4 myr after the extinction, suggesting a major increase in surface water productivity.

Duration of recovery

The environmental stresses that caused extinction at the K–T boundary appear to have significantly delayed the postextinction recovery. Bivalve and gastropod families which had moderate to high Cretaceous diversity typically did not recover to the diversity of Upper Cretaceous assemblages until the Middle Eocene, ≈20 myr after the K–T boundary. Planktic foraminifera required about 10–15 myr to approach pre-extinction species diversities, as did calcareous nannoplankton and dinoflagellates. In each of these planktic groups, species diversity rebounded within 2–3 myr of the extinction to a level about half that of the Late Cretaceous. A second increase in species richness occurred in the Early Eocene when the planktic groups finally approached pre-extinction diversity. Both the calcareous nannoplankton and planktic foraminifera developed a distinctive 'Paleocene fauna' with a species richness about half that of the Late Cretaceous (Fig. 2.4.5.1). A similar minor rise in species diversity is also observed in the mollusc families Tellinidae and Turritellidae. These Paleocene assemblages are partly replaced during the subsequent Eocene radiation. The recovery to pre-extinction diversities in a number of groups apparently involved a series of separate bursts of diversification rather than logistic diversification from the founding survivors.

Ecological redeployment was often very rapid, but re-establishment of the broad suite of ecologies occupied in the Late Cretaceous often required several million years. For instance, the rebound of reef ecosystems is judged to have taken 5–10 myr following the K–T extinction of reef biotas, as in other mass extinctions during the Phanerozoic (Jablonski 1995). Large increases in the intensity of naticid drilling in the Early Paleocene suggest that the extinction may have selectively removed drilling-resistant species. Among the planktic foraminifera, diversification started immediately in both surface-water and thermocline habitats from lineages that survived within them (D'Hondt *et al.* 1996). Notably, the initial radiation of surface-dwelling serial-coiled foraminifera was short-lived and about one-third of the clade's diversity was lost within ≈4 myr of the boundary. On the other hand, descendants of the thermocline survivors in the genus *Hedbergella* diverged into three main stocks within less than 50 kyr, and within a short time had reinvaded surface ocean habitats. Other ecologies present in the Cretaceous, such as photosymbiosis in planktic foraminifera, were lost during the extinction and were not rediscovered until ≈4 myr after the K–T boundary (Norris 1996). Likewise, the re-establishment of species similar to the largest Cretaceous taxa required ≈15 myr, and even then a diverse, large-sized microbiota did not reappear until the Middle Eocene (≈20 myr post K–T).

Implications

The K–T extinction removed a considerable part of the food chain, leading to a drastic, long-lived reorganization of nutrient and biogeochemical cycling in the marine realm. The ≈500 kyr interval of opportunistic blooms by various groups of plankton and depressed carbonate accumulation rates suggest that key parts of marine ecosystems had to be replaced by evolution, and not just by regrowth of populations after the K–T event. Likewise, very low carbon isotope gradients between surface and deep waters may indicate that the organisms ordinarily responsible for exporting carbon into deep water were absent for an extended period (several million years). In addition, the extremely long duration of unusual carbon cycling in the oceans suggests that the

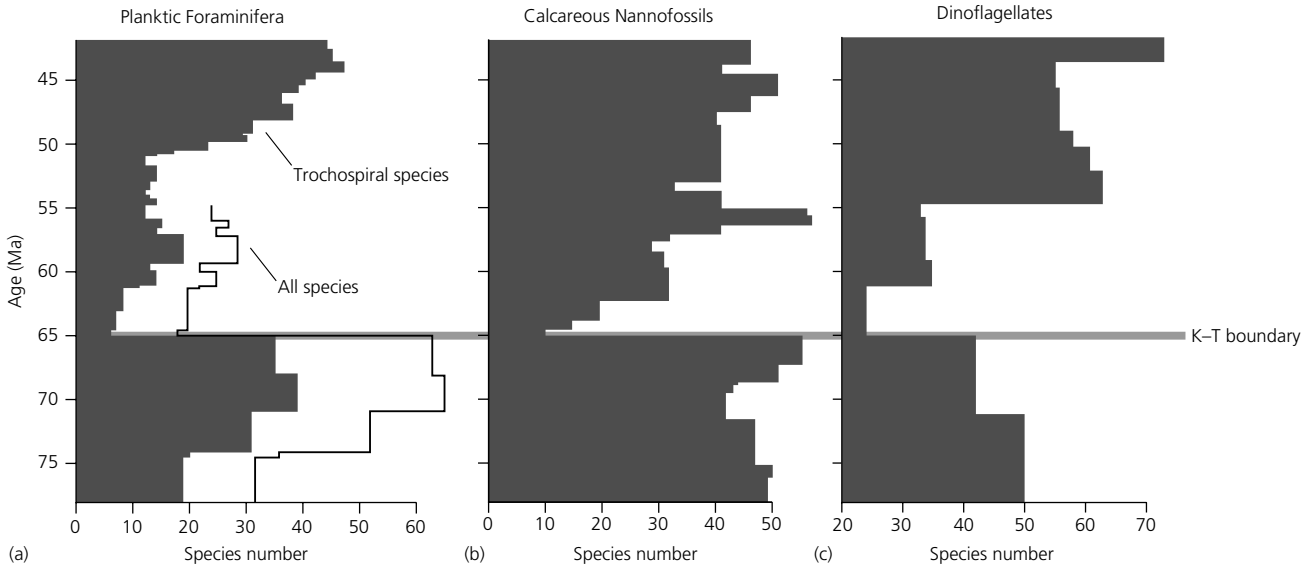

Fig. 2.4.5.1 Species diversities of planktic foraminifera, calcareous nannofossils, and dinoflagellates across the K–T boundary; note initial diversification in the Paleocene (65–56 Ma) in each group, reaching species richness about half that in the Cretaceous. (a) Planktic foraminifera diversity shown for trochospirally coiled species (Norris 1996) and for all species, including serially coiled taxa (compiled by the author). (b) Nannoplankton diversity includes about two-thirds of estimated species diversity and probably overestimates the rise in species richness near 55 Ma. (c) Dinoflagellate diversity.

extinction may have had drastic and widespread effects on oceanic plankton as a whole, not just those taxa with a substantial fossil record.

The initial radiation produced morphological novelties unknown from the Cretaceous, but did so while species diversities were still low; apparently it was easier for novelties to be established in the early Danian than in the late Maastrichtian. Re-establishment of pre-extinction morphological, taxonomic, and ecological diversity was achieved through a series of radiations rather than a single sustained event. The low species richness of some clades during the Paleocene suggests that these may have included less specialized taxa than those which evolved during the subsequent diversification in the Early Eocene. The 10–15 myr delay in re-establishing Cretaceous levels of species diversity and body size implies that the timing of the radiations may have been influenced by the waiting time to acquire novelties as well as the stimulating effects of subsequent climatic changes, such as the onset of the Early Eocene warm period.

References

D'Hondt, S., Herbert, T.D., King, J. and Gibson, C. (1996) Planktic foraminifera, asteroids, and marine production: death and recovery at the Cretaceous–Tertiary boundary. *Geological Society of America Special Paper* **307**, 303–317.

Jablonski, D. (1995) Extinctions in the fossil record. In: J.H. Lawton and R.M. May, eds. *Extinction rates*, pp. 25–44. Oxford University Press, Oxford.

Kelley, P.H. and Hansen, T.A. (1996) Recovery of the naticid gastropod predator–prey system from the Cretaceous–Tertiary and Eocene–Oligocene extinctions. In: M.B. Hart, ed. *Biotic recovery from mass extinction events*, pp. 373–386. Geological Society, London.

MacLeod, N., Rawson, P.F., Forey, P.L., Banner, F.T., Boudagher-Fadel, M.K., Bown, P.R., Burnett, J.A., Chambers, P., Culver, S., Evans, S.E., Jeffery, C., Kaminski, M.A., Lord, A.R., Milner, A.C., Milner, A.R., Morris, N., Owen, E., Rosen, B.R., Smith, A.B., Taylor, P.D., Urquhart, E. and Young, J.R. (1997) The Cretaceous–Tertiary biotic transition. *Journal of the Geological Society* **154**, 265–292.

Norris, R.D. (1996) Symbiosis as an evolutionary innovation in the radiation of Paleocene planktic foraminifera. *Paleobiology* **22**, 461–480.

Smith, A.B. and Jeffery, H. (1998) Selectivity of extinction among sea urchins at the end of the Cretaceous period. *Nature* **392**, 69–71.

Speijer, R.P. and van der Zwaan, G.J. (1996) Extinction and survivorship of southern Tethyan benthic foraminifera across the Cretaceous/Paleogene boundary. In: M.B. Hart, ed. *Biotic recovery from mass extinction events*, pp. 343–371. Geological Society, London.

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2.4.6 Impact of K–T Boundary Events on Terrestrial Life

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Introduction

Events at the Cretaceous–Tertiary (K–T) boundary profoundly affected terrestrial environments and their biota. They are best documented in sediments in the Northern Hemisphere and more particularly in North America. The biotic consequences of the boundary events have typically been cast in terms of extinction. Thus, arguments over whether, for example, the dinosaurs and/or ammonites became extinct at the K–T boundary or had died out largely or entirely before, have consumed much paper. Equally unenlightening are discussions of faunal and floral 'turnovers' that preceded or coincided with boundary events and may have reflected long-term changes in climate or geography. Such discourse is essentially irrelevant to determining whether one or more major catastrophic bolide impacts occurred at the K–T boundary and assessing their environmental effects. The logical progression should be to look for evidence of environmental disruption in the physical and/or biological records at the boundary and then to analyse how it may have caused extinctions, and in turn rediversification.

Physical changes and evidence

The occurrence of at least one major bolide impact at the K–T boundary 65 myr ago is well documented (Alvarez 1997). Theoretical considerations suggest that among the physical consequences of a major impact were (1) attenuation of solar radiation, either from impact-related solid debris or the injection of massive amounts of water into the upper atmosphere and consequently (2) a period of intense cold (Alvarez 1997). Further, (3) oceanic margins may have been subjected to major tsunamis and (4) acid rains of hours to months duration (Alvarez 1997). At one midlatitude site in North America, plant tissues show microstructure that has been experimentally duplicated by freezing (Wolfe 1999). Tsunami deposits are present in some areas and alteration of boundary sediments is consistent with acidic environments. However, there is no evidence, such as a major increase in deposition of charcoal, for the massive forest fires postulated for the immediate postimpact terrestrial environment (Alvarez 1997).

One bolide or more?

North American sites where impact debris is found are typically associated with an abrupt increase in fern spores in the palynological record, the so-called 'fern spike'. This is interpreted as evidence of a major ecological disruption (Upchurch 1989), with ferns representing the recovery vegetation (as on Krakatoa). Discovery of the Chicxulub impact structure in Yucatan suggests that some physical and biological effects may have been confined primarily to the region of North America. Large shock-metamorphosed quartz and microtektites are indeed prominent in the North American K–T boundary sections. However, some biological evidence has not been addressed. At K–T boundary sections, such as the Raton Basin Madrid East site and the Powder River Basin Dogie Creek, Sussex and Teapot Dome sites, the fern spike is found within the boundary claystone or the 'impact' bed that contains the shock-metamorphosed quartz and high iridium levels. The fern spike must postdate the event—the major bolide impact and consequent impact winter—by several weeks, i.e. the ferns killed back to rhizomes would need at least three to four weeks following the end of the impact winter to reach sporing stage. Thus the impact debris seemingly most related to the Chicxulub bolide—the large shock-metamorphosed quartz and the microtektites—appears to be unrelated to the bolide that caused the impact winter and associated fern spike. If the Chicxulub structure was indeed too small to have produced the impact winter (Morgan *et al.* 1997), perhaps it was caused by a larger oceanic impact at a site long since subducted (cf. Alvarez 1997). Thus the effects of the impact winter need not have been largely confined to North America, and the record in North America could serve as a model for other regions.

Environmental and biotic changes near the K–T boundary

Leaf assemblages near the K–T boundary show that the late Maastrichtian was warmer than the earlier Maastrichtian (Upchurch 1989; Wolfe 1997). This is reflected in vertebrate distributions, which show a northward intrusion of a southern, sauropod-dominated fauna of South American affinities (Lehman 1997). A recent attempt to document a major temperature decline from the latest Maastrichtian into the Early Paleocene is based upon questionable palaeobotanical data and the low mean annual temperature (6.3°C) proposed for the stratigraphic interval containing abundant crocodilians is one under which no living crocodilians can survive (Wolfe 1999).

The environmental effects immediately following the K–T boundary that are considered best documented are: (1) a short-term (1–2 months maximum) lowering of

temperatures to near- or below-freezing levels at middle to high latitudes of the Northern Hemisphere, which occurred during the summer; (2) a subsequent greenhouse warming, which persisted for perhaps 0.5–1 myr; and (3) a major increase in precipitation, especially in middle latitudes (Upchurch 1989). Preliminary multivariate analysis of leaf physiognomy suggests that a significant temperature increase occurred at middle latitudes in the western interior of North America following the impact winter (Wolfe 1997). Although some of the leaf assemblages analysed are insufficiently diverse to yield accurate estimates, at least some warming appears probable.

During the Paleocene, precipitation remained well above latest Cretaceous levels, as evidenced by analyses of leaf physiognomy. Further indication of high run-off immediately above the K–T boundary in the Raton Basin is indicated by the barren series, composed mostly of channel sandstones and little coal; and in the Powder River and Williston basins to the north, massive channel sands also occur in the interval above the boundary. Precipitation probably increased three- or four-fold from a somewhat dry climate, supporting a fairly opencanopy vegetation during the Maastrichtian, to a climate supporting a dense, closed-canopy (and presumably multistratal) rain forest throughout much of midlatitude North America (and presumably Eurasia also). These forests were no longer browsed by megaherbivores.

Extinctions and recovery

A significant problem in evaluating extinction and/or origins of terrestrial plants arises from the limitations of palynological studies. Pollen of extant angiosperms is rarely determinable to species and often even to genus by ordinary light microscopy. Thus, survival of a single pollen species could mask actual extinction of many biological species (Upchurch 1989). Because of the difficulty in determining extinction levels from palynological data, claims for little or no extinction in areas such as Seymour Island, Antarctica, must be viewed with scepticism, especially when the high iridium levels and shock-metamorphosed minerals (even if small) are absent, suggesting that deposition across the K–T boundary was discontinuous.

Certainly palynomorph and leaf floras of the Maastrichtian are very diverse. Estimates of extinction of terrestrial flora at the K–T boundary in the western interior of North America are approximately 45% of palynomorph 'species', probably reflecting generic-level extinction (Upchurch 1989). Approximately 75% of leaf species underwent extinction in broadleaved evergreen vegetation in the Raton Basin of New Mexico and adjacent Colorado (Upchurch 1989), but extinction levels appear to have been somewhat lower at higher latitudes. Early Paleocene palynomorph and leaf assemblages are notably of low diversity. During the Paleocene diversity increased dramatically, both in the pollen and leaf records. Indeed, family-level originations appear to have reached their highest level during the Paleocene (Wolfe 1997). The combination of extinctions at the K–T boundary and large areas of abundant rainfall during the early Tertiary probably provided impetus for high levels of diversification.

Patterns in the vertebrates approximately parallel those in terrestrial plants. Overall levels of dinosaur diversity and abundance of preservation show no evidence of severe decline during the Maastrichtian relative to mid-Campanian levels (White *et al.* 1998). Dinosaurs probably had higher metabolic rates than extant reptiles but almost certainly less than modern mammals (Russell 1996). Stressed animals—and especially the metabolically somewhat handicapped dinosaurs—would have decreased in size if cooling occurred during the Maastrichtian in association with less productive vegetation, but no such size reduction is evident in the late Maastrichtian dinosaurs of North America.

Evidence of major forest fires is absent in North America, whereas decay was common (cf. sapropels; Upchurch 1989), and probably catalysed by increased rainfall. Detritivores survived the boundary events reasonably well, whereas animals dependent upon green plant productivity suffered dramatic extinctions. Herbivore extinctions seemingly resulted from starvation rather than freezing, and as the herbivores perished so also did the carnivores.

As in the case of floras, mammals underwent a dramatic Paleocene radiation. First occurrences for some groups almost immediately followed the K–T boundary, probably as a result of immigration from areas where the extinctions were less severe and previous adaptation to dense rain-forest environments. Significantly, many lineages of mammals show a marked increase in body size following the K–T boundary, a probable response to entry into the large-herbivore niche previously vacated by dinosaurs (Alroy 1998).

References

Alroy, J. (1998) Cope's rule and the dynamics of body mass evolution in North American fossil mammals. *Science* **280**, 731–734.

Alvarez, W. (1997) T. rex *and the Crater of Doom*. Princeton University Press, Princeton, New Jersey.

Lehman, T.M. (1997) Late Campanian dinosaur biogeography in the Western Interior of North America. In: D.L. Wolberg, D.E. Stump and G.D. Rosenberg, eds. *Dinofest International: Proceedings of a symposium held at Arizona State University*, pp. 223–240. Academy of Natural Sciences, Philadelphia.

Morgan, J., Warner, M., Brittan, J., Buffler, R., Camargo, A., Christeson, G., Denton, P., Hildebrand, A., Hobbs, R., Macin-

tyre, H., Mackenzie, G., Maguire, P., Marin, L., Nakamura, Y., Pilkington, M., Sharpton, V., Snyder, D., Suarez, G. and Trejo, A. (1997) Size and morphology of the Chicxulub impact crater. *Nature* **390**, 472–476.

Russell, D.A. (1996) The significance of the extinction of the dinosaurs. In: G. Ryder, D. Fastovsky and S. Gartner, eds. *The Cretaceous–Tertiary event and other catastrophes in Earth history. Geological Society of America Special Paper* **307**, 381–388.

Upchurch, G.R. (1989) Terrestrial environmental changes and extinction patterns at the Cretaceous–Tertiary boundary, North America. In: S.K. Donovan, ed. *Mass extinctions: processes and evidence*, pp. 195–216. Columbia University Press, New York.

White, P.D., Fastovsky, D.E. and Sheehan, P.M. (1998) Taphonomy and suggested structure of the dinosaurian assemblage of the Hell Creek Formation (Maastrichtian), eastern Montana and western North Dakota. *Palaios* **13**, 41–51.

Wolfe, J.A. (1997) Relations of environmental change to angiosperm evolution during the Late Cretaceous and Tertiary. In: I. Iwatsuki and P.H. Raven, eds. *Evolution and diversification of land plants*, pp. 269–290. Springer-Verlag, Tokyo.

Wolfe, J.A. (1999) 'Early Palaeocene palaeoclimatic inferences from fossil floras of the western interior, USA'—comment. *Palaeogeography, Palaeoclimatology and Palaeoecology* **150**, 343–345.

2.4.7 Pleistocene Extinctions

K. ROY

Introduction

The Pleistocene (≈1.8–0.01 Ma) fossil record accumulated during a series of glacial and interglacial episodes and has contributed greatly to our understanding of how species and communities respond to climatic changes. One of the most surprising insights derived from the Pleistocene record is the failure of average extinction rates to rise above background for most groups of organisms, despite the extreme climatic fluctuations. For the Pleistocene as a whole, per taxon extinction rates for terrestrial mammals do not appear to be exceptionally high compared with the rest of the Cenozoic, and the same is true for North American amphibians and reptiles (e.g. Alroy 1999). Insects have a rich Pleistocene fossil record but very few extinct species are known from this period (Coope 1995). The Pleistocene pollen records show ample evidence of species shifting their geographical distributions in response to climatic change, but do not reveal heightened global extinctions of plant taxa. Among marine organisms, western Atlantic and Caribbean molluscs and reef-corals do show high levels of extinction during the latest Pliocene and the earliest Pleistocene, but extinction rates did not rise above background for the rest of the Pleistocene (Budd *et al.* 1996). Similarly, Pleistocene extinction rates for eastern Pacific molluscs are not significantly different from the background rate for the Neogene. In general, the Pleistocene fossil record provides ample evidence of local extinctions and individualistic movements of species in response to climatic changes, but very little evidence for global extinction of species (Coope 1995; Roy *et al.* 1996).

Patterns of Late Pleistocene mammalian extinctions

While the overall extinction rates for the Pleistocene do not appear to be exceptionally high for most organisms, one event that does stand out is the terminal Pleistocene extinction of the terrestrial mammalian megafauna (taxa with mean adult body weight greater than 44 kg). This extinction event appears to be global in scope, although the magnitude of the extinctions varied markedly between continents (Martin 1984; Stuart 1991). Highest losses were in North America (33 out of 45 genera lost), South America (46 out of 58 genera), and Australia (15 out of 16 genera) (Martin 1984). In North America the extinct taxa include sabre-toothed cats (*Smilodon*, *Homotherium*), mastodon (*Mammut*) and mammoths (*Mammuthus*), short-faced bear (*Arctodus*), camel (*Camelops*), horse (*Equus*), giant armadillo (*Holmesina*), glyptodonts (*Glyptotherium*), and ground sloths (*Megalonyx*, *Eremotherium*, *Nothrotheriops*, *Glossotherium*). South American extinctions include gomphotheres, ground sloths, glyptodonts, horses, and large notoungulates (*Mixotoxodon*, *Toxodon*). The Late Pleistocene in Australia saw the demise of a number of giant marsupials, including the diptrodonts (e.g. *Diptrodon*, *Zygomaturus*, and *Nototherium*), giant kangaroos (*Macropus titan*, *M. ferragus*), and large carnivores such as the marsupial lion (*Thylacoleo*). Extinction magnitudes were somewhat lower in Europe (7 of 24 genera) and lowest in Africa (7 of 49 genera for the whole of Africa, and 2 of 44 for Africa south of the Sahara) (Stuart 1991).

The intercontinental differences in extinctions become even more apparent when mammals weighing over 1000 kg are considered. In this size category, North America lost all four genera (with five species) in the Late Pleistocene, Europe lost four out of five genera, but Africa lost none (Stuart 1991). The Late Pleistocene mammalian extinctions also affected taxa other than those in the megafaunal size category. A 75% loss of large mammalian genera in the American tropics during the Late Pleistocene has been estimated, with only 4 of 23 known genera of the Amazon basin surviving (Webb and Rancy

1996). The Late Pleistocene also saw pronounced extinctions of small vertebrates on islands (Martin 1986). In addition, despite the relatively poor fossil record of continental birds, at least 12 extinct genera of birds are known from the Wisconsin age of North America (mostly from the Rancho La Brea deposits) (Stuart 1991). These extinct birds tend to be relatively large (including giant teratorns with wingspans of up to 5 m), and were mostly raptors and/or scavengers.

While generic patterns of extinction are well documented for Late Pleistocene mammals, species-level patterns are less well known for most continents. This poses a problem in comparing the patterns of extinctions across the body size spectrum, especially as a small number of species, but very few genera, of small mammals also became extinct at the end of the Pleistocene (Stuart 1991). However, the available data suggest that the percentage of small mammals that became extinct is much lower than that of large mammals (Stuart 1991). Given the selective pattern of extinctions among vertebrates (and the lack of heightened extinctions in invertebrates), the Late Pleistocene extinctions do not classify as a mass extinction event (Martin 1986). However, these extinctions were certainly catastrophic for large terrestrial mammalian communities in the Americas and in Australia, and forever changed the structure of these communities.

Causes of extinctions

While the patterns of Late Pleistocene mammalian extinctions are relatively well documented, the causes of these extinctions remain a subject of debate. A number of explanations, invoking mechanisms ranging from astronomical factors to disease outbreak, have been proposed, but at present there are two main contending hypotheses: the effects of climatic change and/or the effects of human predation (Martin 1986; Stuart 1991). There is general agreement that the Late Pleistocene mammalian extinctions occurred against a backdrop of significant climatic change and increasing predation from human populations, but their relative importance in driving the extinctions remains a matter of contention (Stuart 1991).

Climatic explanations

The end-Pleistocene transition from a glacial to an interglacial climate resulted in extensive reorganization of plant communities; mosaic vegetational communities were replaced by climatically zoned vegetation like that of today (Stuart 1991). The 'coevolutionary disequilibrium' model (Graham and Lundelius 1984) views climate-related changes in vegetation as the main driving force in Late Pleistocene extinctions. According to this view, the Late Pleistocene terrestrial vertebrate communities were highly coevolved and disintegrated when the climatic and vegetational changes forced each species to respond individualistically (Graham and Lundelius 1984; Stuart 1991). Under this scenario, herbivores that had evolved to feed on a wide range of plants (i.e. needed a vegetational mosaic) would have disappeared first, and in turn would have led to the extinction of the large carnivores and scavengers that depended on them (Graham and Lundelius 1984). While it is undoubtedly true that mammalian species responded individualistically to Late Pleistocene climatic changes (FAUNMAP Working Group 1996), the main problem with the climatic hypothesis is the lack of significant global extinctions associated with earlier Pleistocene glacial–interglacial transitions (Alroy 1999). It has been argued that the climatic change during the latest Pleistocene was fundamentally different from earlier glacial–interglacial transitions (Graham and Lundelius 1984) but the evidence for this contention remains equivocal, especially in the light of recent palaeoclimatic data (Roy *et al*. 1996; Alroy 1999).

The overkill hypothesis

In North America the Late Pleistocene extinctions correlate well with the arrival of anatomically modern humans, and hunting by early people has been proposed as the main driving force behind the extinctions (Martin 1984, 1986). The diachronous nature of the megafaunal extinctions on a global scale, with extinctions on different continents roughly coinciding with the arrival of humans, has been cited as supporting evidence for this hypothesis (Fig. 2.4.7.1) (Martin 1984). Radiocarbon dates from North America, south of the ice sheets, suggest that the megafaunal extinctions occurred within a fairly short time interval (≈11 500–10 500 BP) and coincided with the arrival of the Clovis people (Stuart 1991). However, reliable radiocarbon dates are still lacking for many taxa, as well as certain regions, and hence synchroneity of the extinctions has yet to be demonstrated (Stuart 1991).

One problem in using the timing of extinctions to distinguish the effects of hunting from those of climate change is that in North America the arrival of Clovis hunters and changes in vegetation happened within a very short period of time (Stuart 1991). Other criticisms of the overkill hypothesis cite the lack of correlation between the arrival of anatomically modern humans and extinction in Eurasia; for example, upper palaeolithic hunters were probably present in western Europe by about 35 000 BP but the megafaunal extinctions happened between 13 000 and 10 500 BP (Stuart 1991). The rarity of the association of Clovis artefacts and Late Pleistocene megafaunal remains in North America has also been

Afroeurasia: No major episodes of extinction during past 100 000 years, although some losses occurred

Meganesia: Humans arrive 40 000–60 000 BP; major extinction episode follows, but extends to ≈15 000 BP (or later?)

Americas: Ecologically significant human populations arrive 12 500 BP; major extinction episode terminates ≈10 500 BP, few extinctions thereafter

Mediterranea: Humans arrive 10 000 BP; major extinction episode follows and terminates ≈ 4000 BP, few extinctions thereafter

Antillea: Humans arrive 7000 BP; major episode of extinction follows, but extends to ≈ AD 1600 (or later?)

Madagascar: Humans arrive 2000 BP; major episode of extinction follows and terminates ≈ AD 1500, few extinctions thereafter
Mascarenes (Ms): Humans arrive AD 1600; major episode of extinction follows and terminates ≈ AD 1900
New Zealand: Humans arrive 800–1000 BP; major episode of extinction follows and terminates ≈ AD 1500

Commander Islands (C): Humans arrive AD 1741; Steller's sea cow extinct by AD 1768
Wrangel Island (W): Humans arrive ?; mammoths survive to 4000 BP
Galápagos Islands (G): Humans arrive AD 1535; modern-era extinctions only

used to argue against the overkill hypothesis. However, computer simulation of human hunting has suggested the possibility of a 'blitzkrieg' effect: the rapid disappearance of the megafauna would explain the lack of a prolonged association with humans in North America. Indeed, if the Late Pleistocene events were anything like a 'blitzkrieg' then the lack of fossil evidence for human predation is to be expected (Martin 1984). On the other hand, a statistical test of the predictions of the 'blitzkrieg' scenario, using the available data, did not support the model (Beck 1996).

Combined climate change and overkill

The debates about the causes of the megafaunal extinctions led to the suggestion that the observed patterns may reflect a combination of climatic changes and human predation. Under this scenario, human predation only became critical once the populations of the large mammalian taxa declined and/or became restricted geographically in response to climatic and vegetational changes (Stuart 1991). This combined model has intuitive appeal and does circumvent some of the criticisms of the overkill hypothesis. However, it is not clear why the populations of large vertebrates would have declined at this time, as the melting of the ice sheets would have substantially increased the available habitable area. Hard data on the exact role of upper palaeolithic peoples in causing the megafaunal extinctions remain elusive (Stuart 1991).

Conclusions

Although there are a number of testable hypotheses about the causes of the Late Pleistocene megafaunal extinctions, proper tests of these ideas are still largely lacking (but see Beck 1996; Alroy 1999), mainly due to inadequate Late Pleistocene faunal and archaeological data from continents other than North America (Stuart 1991). Even in North America, reliable radiocarbon dates, essential for testing the predictions of the overkill hypothesis, are still unavailable for many taxa. Thus the current debate about the causes of the megafaunal extinctions is based mainly on circumstantial evidence, and this situation is unlikely to change without more refined palaeoecological and archaeological data and radiocarbon dates (Stuart 1991). The Late Pleistocene extinctions certainly changed the structure of mammalian communities in the Americas, and the legacy of this event remains today because 10 000 years is not enough time for an evolutionary recovery. Thus a better understanding of the Late Pleistocene mammalian extinctions would provide important insights into the dynamics of present-day terrestrial ecosystems.

Fig. 2.4.7.1 (*Facing page*) Timing of Late Pleistocene and Holocene extinction events on various continents and large islands. The sequence of extinctions correlates well with the spread of prehistoric people. (From Brown and Lomolino 1998.)

References

Alroy, J. (1999) Putting North America's end-Pleistocene megafaunal mass extinction in context: large-scale analyses of spatial patterns, extinction rates, and size distributions. In: R.D.E. MacPhee, ed. *Extinctions in near time: causes, contexts, and consequences*, pp. 105–143. Plenum, New York.

Beck, M.W. (1996) On discerning the cause of late Pleistocene megafaunal extinctions. *Paleobiology* **22**, 91–103.

Brown, J.H. and Lomolino, M.V. (1998) *Biogeography*. Sinauer, Massachusetts.

Budd, A.F., Johnson, K.G. and Stemann, T.A. (1996) Plio-Pleistocene turnover and extinctions in the Caribbean reef-coral fauna. In: J.B.C. Jackson, A.F. Budd and A.G. Coates, eds. *Evolution and environment in tropical America*, pp. 168–204. University of Chicago Press, Chicago.

Coope, G.R. (1995) Insect faunas in ice age environments: why so little extinction? In: J.H. Lawton and R.M. May, eds. *Extinction rates*, pp. 55–74. Oxford University Press, Oxford.

FAUNMAP Working Group (1996) Spatial response of mammals to late Quaternary environmental fluctuations. *Science* **272**, 1601–1606.

Graham, R.W. and Lundelius, E.L. Jr (1984) Coevolutionary disequilibrium and Pleistocene extinctions. In: P.S. Martin and R.G. Klein, eds. *Quaternary extinctions*, pp. 223–249. University of Arizona Press, Tucson, Arizona.

Martin, P.S. (1984) Prehistoric overkill: a global model. In: P.S. Martin and R.G. Klein, eds. *Quaternary extinctions*, pp. 354–403. University of Arizona Press, Tucson, Arizona.

Martin, P.S. (1986) Refuting late Pleistocene extinction models. In: D.K. Elliot, ed. *Dynamics of extinction*, pp. 107–130. Wiley, New York.

Roy, K., Valentine, J.W., Jablonski, D. and Kidwell, S.M. (1996) Scales of climatic variability and time averaging in Pleistocene biotas: implications for ecology and evolution. *Trends in Ecology and Evolution* **11**, 458–463.

Stuart, A.J. (1991) Mammalian extinctions in the late Pleistocene of northern Eurasia and North America. *Biological Reviews* **66**, 453–562.

Webb, S.D. and Rancy, A. (1996) Late Cenozoic evolution of the Neotropical mammal fauna. In: J.B.C. Jackson, A.F. Budd and A.G. Coates, eds. *Evolution and environment in tropical America*, pp. 335–358. University of Chicago Press, Chicago.

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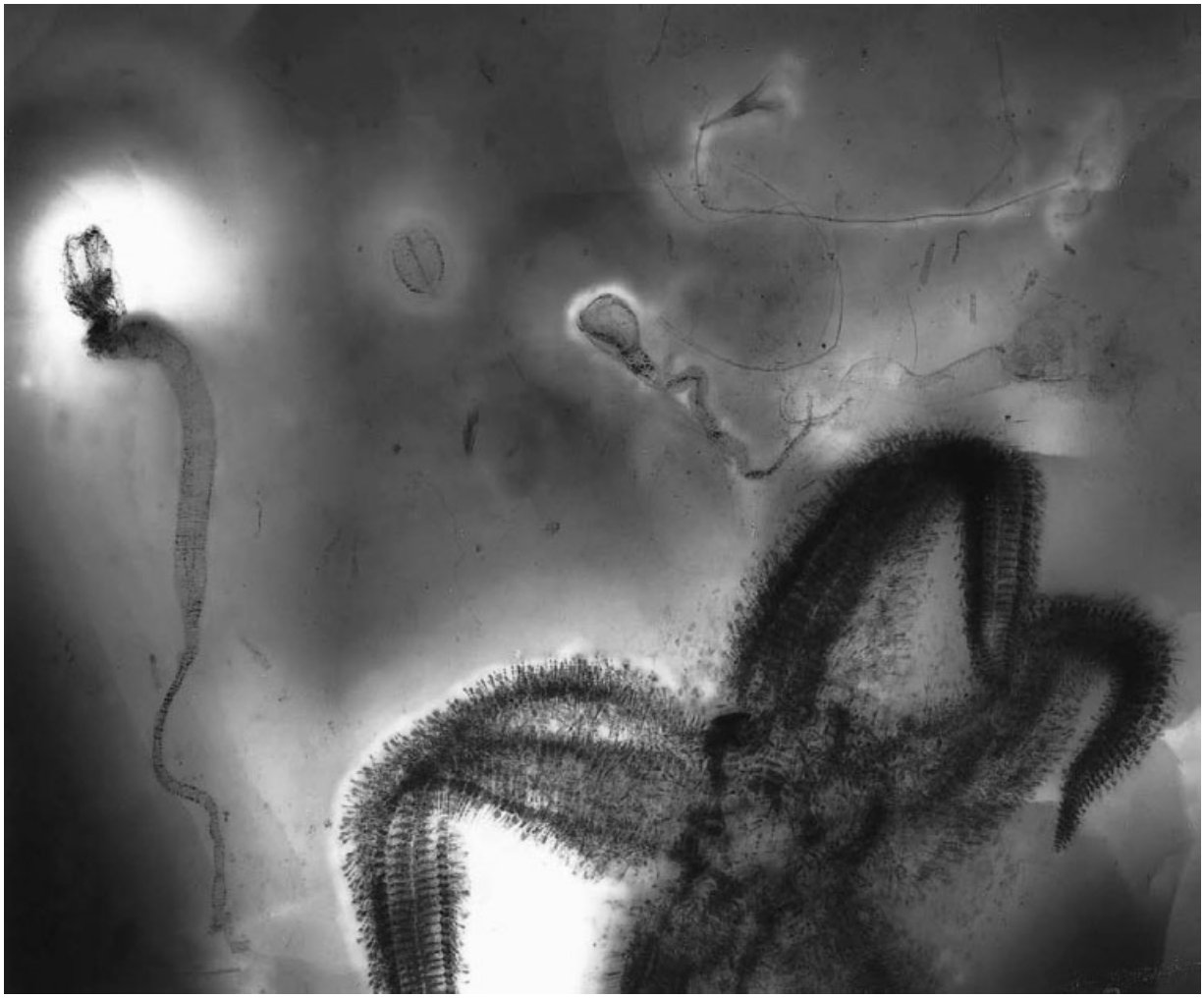
3
TAPHONOMY



X-radiograph showing pyritized fossils (brachiopods with the pedicle preserved, a small arthropod, a crinoid, and a specimen of the asteroid *Echinasterella sladeni*) from the Lower Devonian Hunsrück Slate of Bundenbach, Germany, ×1. (X-radiographed by W. Blind, Giessen; specimen courtesy of M. Poschmann, Mainz.)

3.1 Fossilized Materials

3.1.1 DNA

H.N. POINAR and S. PÄÄBO

Introduction

In principle, the retrieval of DNA from fossils opens up enormous possibilities for the study of molecular evolution since it allows the molecular evolutionist to go back in time, in an analogous fashion to palaeontologists. In addition, if genetic information can be extracted from fossils of known morphology, this allows morphological and molecular evolutionary processes to be studied in conjunction. The oldest DNA sequences that have been reported to date, and subsequently reproduced in other laboratories, are from remains of the woolly mammoth over 50 kyr old found in the Siberian permafrost. The recovery of DNA from fossils that are substantially older remains controversial. In fact, all DNA sequences determined from fossils that are millions of years old have either failed to be reproduced or been derived from identifiable contaminants.

DNA preservation and degradation

The two major factors most likely responsible for difficulties in the retrieval of genuinely ancient DNA are: (1) the degradation of DNA within tissues shortly after death; and (2) the modification and further degradation of nucleic acids that takes place in the depositional environment. Immediate postmortem degradation can be limited if deposition is rapid and particularly if dehydration of the tissues follows quickly upon death. The nature and rates of the diagenetic processes that take place after deposition are more complex. However, some of them can be extrapolated from chemical processes studied in the laboratory over shorter periods of time. It has been suggested, for example, based on studies of the rate of DNA depurination in aqueous solution, that no meaningful genetic information would be preserved for longer than 10 kyr in temperate climates and 100 kyr in colder climates (Pääbo and Wilson 1991; Lindahl 1993). Thus, the observation that DNA sequences older than about 100 Ka cannot be reproducibly retrieved is consistent with current knowledge about the chemical stability of the DNA molecule.

One consequence of the extensive degradation and modification of the DNA extracted from many remains is that only multicopy DNA sequences (e.g. from mitochondria) can be retrieved. Only in rare cases, such as well-preserved permafrost remains (Greenwood *et al.* 1999), can nuclear DNA sequences that occur in just one copy per haploid genome be retrieved. It would obviously be very valuable if this could be done in more cases, and progress with the repair of DNA present in fossils may make it possible, as well as the retrieval of DNA sequences from some samples hitherto unavailable for molecular analysis. For example, Late Pleistocene coprolites contain products of the Maillard reaction, i.e. the condensation reaction between reducing sugars and amino groups in macromolecules such as proteins and DNA (Poinar *et al.* 1998). A chemical compound which cleaves cross-links derived from the Maillard reaction allowed DNA to be amplified from a 20-kyr-old ground sloth coprolite from Gypsum Cave, Nevada (Poinar *et al.* 1998), which had previously failed to yield any endogenous DNA. Further characterization of molecular modifications in ancient DNA (e.g. Höss *et al.* 1996; Poinar *et al.* 1998), and the application of repair strategies designed to remove the modifications detected, should lead to further progress in the retrieval of authentic DNA.

Criteria of authenticity

Most remains of bone and soft tissues found at archaeological and palaeontological sites do not contain endogenous DNA that can be examined successfully using current techniques for extraction and amplification via the polymerase chain reaction (PCR). Instead, remains often contain DNA from exogenous sources, such as bacteria and fungi, as well as from contemporary humans (Handt *et al.* 1994). For any work involving ancient DNA it is critical to ensure, as far as possible, that the DNA sequences determined are indeed endogenous to the specimen and not derived from contamination by more recent or contemporary DNA. A useful consideration in this context is the observation that conditions of preservation should have been similar for all macromolecules in any particular sample from a specimen. Thus, DNA, which is generally more sensitive to hydrolytic and oxidative processes than many other macromolecules (such as proteins, carbohydrates, and lipids), is unlikely to be preserved in specimens where other classes of molecules have not survived. Based on this consideration, as well as the tenet that scientific results should be reproducible, criteria of authenticity for ancient DNA have

been suggested (Table 3.1.1.1: Criteria 1–8) (e.g. Handt *et al.* 1994).

Aspects of amino acid preservation have been shown to correlate with DNA preservation. Since amino acids can be readily analysed from small samples of palaeontological and archaeological specimens (Poinar *et al.* 1996; Poinar and Stankiewicz 1999), they are very useful, both for screening large numbers of samples before DNA extraction and for verifying that DNA might be preserved in a specimen (Criterion 1). Negative controls (Criterion 2) are obviously a necessary part of every experiment. An inverse correlation of amplification strength with length of amplicon (Criterion 3) indicates that the template is degraded and/or modified. This is consistent with it being old but does not rule out the possibility that it represents a degraded modern template. Quantifying the numbers of template molecules initiating an amplification (Criterion 4) is useful. When few molecules initiate the reaction, sporadic contaminations are difficult to exclude and direct sequencing of the PCR product is impossible (Handt *et al.* 1994). Rather, it has to be cloned and many clones must be sequenced in order to detect heterogeneity in the product. The use of overlapping primers (Criterion 5) makes the inadvertent amplification of a mitochondrial DNA sequence inserted in the nuclear genome unlikely. The demonstration of reproducibility (Criteria 6–8) is crucial. However, if results can be reproduced between extracts, it is not necessary to demonstrate reproducibility within extracts. Finally, for human remains (where contamination of modern human DNA is a particularly serious threat) and for any extraordinary or unusual findings, the criteria for authenticity should include reproduction by another laboratory (Criterion 8). This has been done, for example, for the DNA sequences from the 5200-year-old 'Iceman' and the Neandertal type specimen (Table 3.1.1.2). Unfortunately, all other ancient human DNA sequences published to date, and also some animal DNA sequences where independent reproduction would have been useful, have not been authenticated by this criterion, nor by several of the others listed in Table 3.1.1.2. It is therefore hard to judge the reliability of many of these results.

Any future results that fulfil all the criteria listed in Table 3.1.1.1 would clearly be highly reliable. In some cases, however, it may not be necessary to meet all the criteria in order to have confidence in a result. When several well-preserved individuals of an animal species are studied, for example, it is not always necessary to satisfy Criteria 3, 4, and 5 for all individuals. Alternatively, it might be possible to limit the number of reproductions (Criteria 6–8) if a sufficient number of molecules initiate the amplifications (Criterion 4).

Environments conducive to DNA preservation

Since most archaeological and palaeontological remains do not contain enough endogenous DNA for analysis, it would be useful to identify the environmental conditions where the likelihood of preservation is largest. Twenty-six locations from which fossil specimens have yielded endogenous DNA that satisfies most of the criteria in Table 3.1.1.1 (and/or other more arbitrary considerations)—and is therefore regarded as genuine—are plotted in Fig. 3.1.1.1. They are broadly categorized according to whether they were found in permafrost, caves, tar pits and peat bogs, or in soil burials (Table 3.1.1.2).

Table 3.1.1.1 Criteria of authenticity for ancient DNA.

1	**Extent of aspartic acid racemization (D/L < 0.15)** Total amount of amino acids, their composition and relative extents of racemization should indicate whether endogenous amino acids predominate in the specimen (Poinar *et al.* 1996)
2	**No PCR products in negative controls for DNA extraction and amplification** Generally, several PCR controls are necessary in order to detect sporadic or low-copy-number contaminations
3	**Inverse correlation of strength of PCR products to their length** PCR products over 500–1000 bp are generally not achievable
4	**More than 1000 DNA template molecules initiate the PCR** Lower numbers generally make it impossible to exclude the occurrence of sporadic contaminations, especially when human DNA is studied
5	**At least two primer pairs yield the same sequence in overlapping segment of mitochondrial amplicon** The use of different primer pairs makes it highly unlikely that one and the same nuclear insertion of mtDNA would be preferentially amplified by both sets of primers. Furthermore it makes contamination by a PCR product unlikely
6	**Reproducibility of results from the same extract**
7	**Reproducibility from more than one extract**
8	**Reproducibility an independent laboratory** This is particularly important for any novel or unexpected results, as well as for human remains

mtDNA, mitochondrial DNA; PCR, polymerase chain reaction.

Table 3.1.1.2 Samples, ages, locations and references of fossils from which DNA has been retrieved. Numbers refer to Fig. 3.1.1.1.

No.	Taxon	Age (Ka)	Location	Reference
Permafrost				
1	Ice man *Homo sapiens*	5	Tyrolean Alps, Italy	Handt *et al.* (1994) *Science* **264**, 1775
2	Mammoth *Mammuthus primigenius*	9.7	Yuribei, Siberia	Höss *et al.* (1994) *Nature* **370**, 333
3	Mammoth *M. primigenius*	20	Alaskan Steppe, Fairbanks, USA	Yang *et al.* (1996) *Proc. Natl Acad. Sci. USA* **93**, 1190
4	Mammoth *M. primigenius*	25	Taimyr Peninsula, Siberia	Noro *et al.* (1998) *J. Mol. Evol.* **46**, 314
5	Selerikan horse *Equus hemionus*	25	Fairbanks, Alaska, USA	Höss and Pääbo (1993) *Nucleic Acid Res.* **21**, 3913
6	Mammoth *M. primigenius*	40	Magadan, Siberia	Höss *et al.* (1994) *Nature* **370**, 333 Ozawa *et al.* (1997) *J. Mol. Evol.* **44**, 406
7	Mammoth *M. primigenius*	42	Shandrin, Siberia	Höss *et al.* (1994) *Nature* **370**, 333
8	Mammoth *M. primigenius*	46	Lyakhivskiy Island, Siberia	Yang *et al.* (1996) *Proc. Natl Acad. Sci. USA* **93**, 1190
9	Mammoth *M. primigenius*	>47	Allaikhu, Siberia	Hagelberg *et al.* (1994) *Nature* **370**, 333
10	Mammoth *M. primigenius*	>50	Khatanga, Siberia	Höss *et al.* (1994) *Nature* **370**, 333 Hagelberg *et al.* (1994) *Nature* **370**, 333
Caves				
1	Native American *Homo sapiens*	0.6	Ventana Cave, Arizona, USA	Handt *et al.* (1996) *Am. J. Hum. Genet.* **59**, 368
2	Laysan duck *Anas laysanensis*	1–3?	Lava tubes, Hawaii, USA	Cooper *et al.* (1996) *Nature* **381**, 484
3	Laysan duck *Anas laysanensis*	1–3?	Lava tubes, Hawaii, USA	Cooper *et al.* (1996) *Nature* **381**, 484
4	Moa *Anomalopteryx didiformis*	2–3	Otago, New Zealand	Cooper *et al.* (1992) *Proc. Natl Acad. Sci. USA* **89**, 8741
5	Moa *Magelapteryx didinus*	2–3	Nelson, New Zealand	Cooper *et al.* (1992) *Proc. Natl Acad. Sci. USA* **89**, 8741
6	Moa *Pachyornis elephantopus*	2–3	Canterbury, New Zealand	Cooper *et al.* (1992) *Proc. Natl Acad. Sci. USA* **89**, 8741
7	Moa *Dinornis novaezealandiae*	2–3	Otago, New Zealand	Cooper *et al.* (1992) *Proc. Natl Acad. Sci. USA* **89**, 8741
8	Egyptian mummy *Homo sapiens*	4	Tomb, Egypt	Pääbo *et al.* (1990) *J. Biol. Chem.* **265**, 4718–4721
9	Ground sloth * *Mylodon darwinii*	13	Ultima Esperanza, Patagonia, Chile	Höss *et al.* (1996) *Proc. Natl Acad. Sci. USA* **93**, 181
10	Ground sloth *Nothrotheriops shastensis*	20	Gypsum Cave, Nevada, USA	Poinar *et al.* (1998) *Science* **281**, 402
11	Cave bear *Ursus spelaeus*	25	Preletang Cave, Isere, France	Hänni *et al.* (1994) *Proc. Natl Acad. Sci. USA* **91**, 12336
12	Neandertal *Homo neanderthalensis*	>25?	Neander Valley, Germany	Krings *et al.* (1997) *Cell* **90**, 19
Tar pits/ peat bogs				
1	Human *Homo sapiens*	8	Windover peat bogs, Florida, USA	Doran *et al.* (1986) *Nature* **323**, 803
2	Mastodon *Mammut americanum*	10	Bog, Oakland Co., Michigan, USA	Yang *et al.* (1996) *Proc. Natl Acad. Sci. USA* **93**, 1190
3	Sabre-tooth cat *Smilodon fatalis*	11	La Brea tar pits, California, USA	Janczewski *et al.* (1992) *Proc. Natl Acad. Sci. USA* **89**, 9769
Burials				
1	Native American *Homo sapiens*	1	Peru	Salo *et al.* (1994) *Proc. Natl Acad. Sci. USA* **91**, 2091

* Two different specimens from the same cave.

Fig. 3.1.1.1 Location of the samples yielding ancient DNA listed in Table 3.1.1.2.

It is noteworthy that the oldest DNA sequences determined to date are from the permafrost, where 10 samples have yielded results, two of which have been reproduced from the same specimen. Eight of these are from mammoths, whereas the other two are from a human and a horse. Of these 10 samples (age range 5–50 Ka), five are older than 40 Ka.

There have been 12 reports of DNA isolation from caves and one from a mummy found in an Egyptian tomb (in essence a man-made cave). These remains are from two to 50 times younger than those from the permafrost. Five of the samples are older than 10 Ka (range 13–25 Ka), while the remainder are between 3 Ka and 200 years old. With the exception of the Ultima Esperanza Cave (Patagonia, Chile), all are located in temperate or warm regions.

Reports on the isolation of DNA from mammals found in tar pits and peat bogs include a sabre-tooth cat from La Brea tar pits, California, a mastodon from a Michigan peat bog, and a human brain from a Florida peat bog. The samples from these deposits are four to six times younger than those from the permafrost.

One study serves as a representative of many reports of DNA sequences from burial sites: the amplification of tuberculosis DNA from a Peruvian mummy that is five to 50 times younger than samples from the permafrost. While burials are abundant, the amplification of reproducible DNA sequences from such remains is rare, especially from humans. The reason is that contemporary human DNA often cannot be excluded as a source of the amplification products, especially where the criteria in Table 3.1.1.1 are not satisfied. Even the potentially interesting result listed here has not been rigorously authenticated.

Conclusion

A simple synopsis of ancient DNA reports (Table 3.1.1.2) shows that the preservation of DNA appears to be linked with low ambient temperature. This is not surprising as most chemical reaction rates decrease three or four times for every 10°C decrease in temperature. DNA sequences obtained from fossils in temperate regions such as North America and Europe tend to originate from caves, and relatively few are derived from bogs or burials in soil. Caves can maintain relatively constant low temperatures (4–15°C) and a stable humidity (30–100%) even in environments where ambient temperature and humidity vary drastically.

Although the influence of particular environmental conditions on the preservation of biomacromolecules is poorly understood, preservation of different classes of

macromolecule seems to follow a hierarchy predicted by the relative strength of their chemical bonds. This can be used to evaluate the likelihood of DNA preservation in any particular fossil. Furthermore, within the last 100 kyr, time itself is not the crucial factor for preservation. Rather, the inhibition of the initial postmortem degradation of macromolecules and the long-term depositional environment (especially in terms of temperature) seem to determine the possibility of DNA retrieval from fossils.

References

Greenwood, A.D., Capelli, C., Possnert, G. and Pääbo, S. (1999) Nuclear DNA sequences from Late Pleistocene megafauna. *Molecular Biology and Evolution* **16**, 1466–1473.

Handt, O., Höss, M., Krings, M. and Pääbo, S. (1994) Authenticating ancient DNA. *Experientia* **50**, 524–529.

Höss, M., Jaruga, P., Zastawny, T.H., Dizdaroglu, M. and Pääbo, S. (1996) DNA damage and DNA sequence retrieval from ancient tissues. *Nucleic Acids Research* **24**, 1304–1307.

Lindahl, T. (1993) Instability and decay in the primary structure of DNA. *Nature* **362**, 709–715.

Pääbo, S. and Wilson, A.C. (1991) Miocene DNA sequences—a dream come true? *Current Biology* **1**, 45–46.

Poinar, H.N. and Stankiewicz, B.A. (1999) Protein preservation and DNA retrieval from ancient tissues. *Proceedings of the National Academy of Sciences USA* **96**, 8426–8431.

Poinar, H.N., Höss, M., Bada, J.L. and Pääbo, S. (1996) Amino acid racemization and the preservation of ancient DNA. *Science* **272**, 864–866.

Poinar, H.N., Hofrieter, M., Spaulding, G.W., Martin, P.S., Stankiewicz, B.A., Bland, H., Evershed, R.P., Possnert, G. and Pääbo, S. (1998) Molecular coproscopy: dung and diet of the extinct ground sloth *Nothrotheriops shastensi*s. *Science* **281**, 402–406.

3.1.2 Proteins

M.J. COLLINS and A.M. GERNAEY

Introduction

Proteins are abundant biopolymers, the basic composition and organization of which are shared by all organisms. The importance of proteins to palaeontology lies in: (1) their potential to retain biochemical information, which may give an insight into evolutionary relationships; (2) their stable isotopic composition, giving information about diet and climate; (3) their age, given by the decay of ^{14}C; and (4) the extent of their deterioration (reflected notably in the isomerization of amino acids). Yet the potential for the application of protein geochemistry to palaeontology is questionable, because the survival of informative protein fragments beyond the Pleistocene appears to contradict our understanding of rates of chemical decomposition.

Organization

A hierarchical organization can be identified in protein structures, from the individual amino acid sequence to the complex folded patterns that involve more than one strand (e.g. collagen; Fig. 3.1.2.1). The key to their function is a three-dimensional structure which is governed by the distribution of, and interaction between, 20 different amino acid side-chains. Proteins, like nucleic acids, are phylogenetically informative. Proteins are coded directly by the genome and, consequently, may be used in molecular systematic studies; but protein sequences determined directly from nucleic acids are simpler and cheaper to obtain.

Biological decomposition

Microbial activity is thought to recycle an absolute minimum of 90%, but more typically in excess of 99%, of sedimented organic matter prior to burial. Within this pool, proteins (and carbohydrates) are rapidly decomposed. Following death, cellular tissues undergo a process of self-destruction (autolysis) mediated by hydrolytic enzymes which, in life, function in recycling the cellular components. This autolytic hydrolysis makes the protein more amenable to decomposition by microorganisms. Thus cellular tissues are rarely preserved in the fossil record, unless they are rapidly replaced by mineral.

A prerequisite for the survival of phylogenetically informative but biodegradable biopolymers is a burial environment which prevents or significantly reduces microbial degradation. Factors which retard biodegradation have been exploited by man for centuries to prevent food from spoiling; these include desiccation, cold, and pickling (Collins *et al. in* Stankiewicz and van Bergen 1998). Some structural proteins are more inherently resistant to biodegradation. This group comprises simple repetitive molecules with a high degree of structural order (crystallinity) and chemical bonds (cross-links) between strands. These features render the proteins insoluble and less accessible to enzymes; examples include keratin (found in feathers, hair, wool, horn, and claws), fibrinogen (silk, mollusc shell matrix) and collagen (tendon, hide, antler, teeth, and bones).

Rates of chemical alteration

From a palaeontological perspective, the most common mechanism for protein preservation is the physical

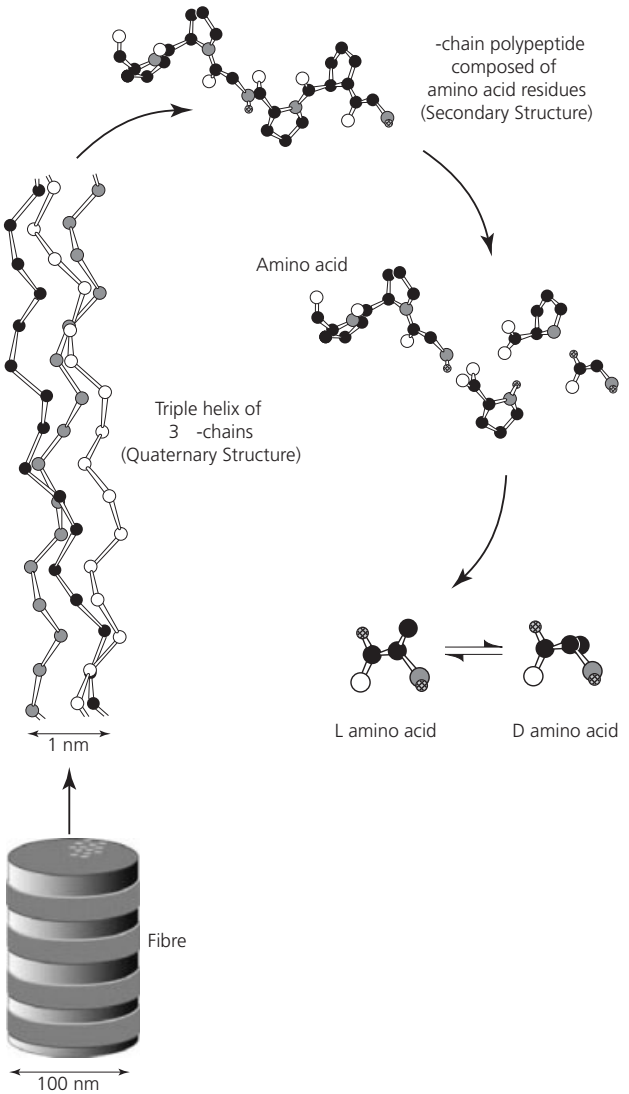


Fig. 3.1.2.1 The levels of organization seen in proteins, in this case collagen. Amino acids are the building blocks of proteins; the sequence of amino acids forms a polypeptide chain. The function of a protein is governed by the complex folding patterns adopted by one or more polypeptide strands. Collagen is a fibrous structural protein in which the strands are braided into a triple helix. The helices themselves are arranged into fibrils, which are then grouped into fibres. The decay of proteins reverses this organizational trend; breakdown of the highly organized tissue leads to increased solubility of the polypeptide strands, which in turn enhances their accessibility to microorganisms. The strands will further decompose chemically to individual amino acids, which can undergo isomerization and further decomposition until the final products are hydrocarbons derived from the carbon backbone.

exclusion of microbial enzymes by biominerals (as in the case of bone collagen or shell matrix proteins). If microorganisms can be excluded, then the rate of degradation of proteins will be governed by chemical alterations, the rates and mechanisms of which are predictable. A limited number of studies have tried to predict the rates at which proteins decay by specific chemical reactions (chapters by Collins *et al*. and Bada *in* Stankiewicz and van Bergen 1998).

Although some peptide-bound residues (such as the aspartyl amide group) undergo rapid decomposition, it appears that the key step in protein decomposition is the breaking of the bonds which join the amino acids together (peptide bond hydrolysis), resulting ultimately in the release of free amino acids. The temperature dependence of peptide bond hydrolysis is well known; in the case of glycine (Gly), a Gly-Gly dipeptide is predicted to have a half-life in water at pH5.6 of 20 kyr at 5°C, declining to 5 kyr at 15°C.

It is possible for the hydrolysis rates to be slowed by reducing the conformational flexibility of a protein, as occurs in the case of mineralized collagen. Collagen is a tough fibrous protein in which three intertwined protein chains produce a triple helix structure (Fig. 3.1.2.1). Estimates of survival indicate that the temperature at which the triple helix melts to form randomly coiled gelatin is raised from 68 to 150°C in bone due to the presence of the mineral. At 15°C (a typical Mediterranean burial temperature), the half-life for destruction of the organized triple helix is estimated to be 30 kyr. These estimates suggest that the rate of peptide bond hydrolysis in bone collagen is slower than estimates derived from pure compounds. Nevertheless, in all but the very coldest climates, preservation even into the Pliocene is unlikely.

Proteins in palaeontology

Various claims for the preservation of protein structure have been made, ranging from intact and active enzymes in Egyptian mummies, intact haemoglobin, to immunologically recognizable fragments of osteocalcin, albumin, and collagen in dinosaur bones. Despite extensive research, none of these findings has satisfied the key criterion used for validation of ancient DNA sequences—independent replication. Many of the claims rely on an interpretation of data determined indirectly; in only one instance has direct sequencing been successfully employed—the sequencing of a fragment of osteocalcin from a 6 Ka moa bone. A direct sequence is the only unambiguous proof of the survival of oligopeptides, but current methods are too readily inhibited by diagenetic modifications to diagnostic residues. Hopefully, new methods—notably time of flight mass spectrometry—will enable direct sequencing of well-preserved ancient proteins.

In the face of failure to sequence proteins, other approaches capable of high sensitivity, coupled with an ability to detect partially degraded proteins, have been used. Most notable are those using antibody detection

(immunological methods). Great care is necessary when using an immunological approach, as has been emphasized by the controversy surrounding the analysis of residues recovered from stone tools.

Similarities between amino acids in some fossils and the distinctive amino acid compositions of structural proteins, notably collagen, have been used to identify protein residues in the fossil record (cf. Towe 1980). The persistence of recognizable distributions of amino acids into the Ordovician is perhaps surprising, but little experimental work has been conducted on their degradation (see Collins *et al*. *in* Stankiewicz and van Bergen 1998), with the notable exception of racemization.

Amino acid isomerization involves the interconversion of left-handed (L) and right-handed (D) isomers (racemization) or an individual chiral carbon in a compound with more than one chiral centre (epimerization). In proteins all amino acids occur as L-isomers (with the exception of glycine, which has no chiral centre), and with time these will interconvert into other isomers until an equilibrium is reached (see Mitterer *in* Engel and Macko 1995). The conversion from one isomeric form to the other obeys kinetic laws; thus the rate of increase of the non-protein isomer should be a function of time and temperature—although the observed rate is influenced by the structure of the protein and its diagenetic history. The most common application of amino acid racemization is as an aid to stratigraphy, using so-called 'aminozones'. These are horizons with similar degrees of isomerization (most often from shelly fauna) which usually represent times of marine transgression during interglacial cycles (see Wehmiller *in* Engel and Macko 1995). Recently this approach has also been used to identify palaeoclimatic change.

Perhaps the most remarkable report of an ancient 'protein' is the ultrastructural preservation of collagen in graptolite periderm (Towe 1980). Fibrous structures are seen with banding patterns, some of which are almost identical to collagen, whereas others display patterns not seen in modern extracellular proteins. Despite the remarkable detail preserved, only trace levels of amino acids have been detected and geochemical investigations suggest a composition dominated by hydrocarbons. This indicates that, if the material was ever proteinaceous, it has undergone considerable modification.

Novel analytical methods capable of determining isotopic ratios in individual amino acids can help to ascertain the origin of amino acids in controversial samples—their so called 'indigeneity'. The detection of protein and non-protein amino acids in meteorites is one such area. Isotopic determinations on individual enantiomers has demonstrated that these amino acids are both abiotic and slightly non-racemic (Engel and Macko 1997)—an analytical *tour de force* which may have implications for the origin of life. Understanding diagenesis will improve racemization-based methods and, more importantly, force a greater realization of the elusive nature of ancient proteins. Despite many claims, we are still a long way from using proteins as palaeontological tools.

References

Engel, M.H. and Macko, S.A., eds. (1995) *Organic geochemistry*. Plenum Press, New York.

Engel, M.H. and Macko, S.A. (1997) Isotopic evidence for extraterrestrial non-racemic amino acids in the Murchison meteorite. *Nature* **389**, 265–268.

Stankiewicz, B.A. and van Bergen, P.F., eds. (1998) *Nitrogen-containing macromolecules in the biosphere and geosphere*. American Chemical Society Symposium Series, No. 707.

Towe, K.M. (1980) Preserved organic ultrastructure: an unreliable indicator for Paleozoic amino acid biogeochemistry. In: P.E. Hare, T.C. Hoering and K. King Jr, eds. *Biogeochemistry of amino acids*, pp. 65–74. Wiley, New York.

3.1.3 Lipids

R.P. EVERSHED and M.J. LOCKHEART

Introduction

Lipids are ubiquitous components of all living organisms and may be present in macrofossil remains provided the burial environment is conducive to their survival. Relatively little is known, however, about the lipid components of fossils, even though their investigation can reveal biogenic organic compounds of clearly defined origin that serve as highly specific carriers of palaeobiological information. The information obtained from such 'biomarker' compounds may reflect palaeoenvironmental conditions and can reveal diagenetic processes. Lipids have been investigated in archaeological material, in the age range of several hundred to a few thousands of years old, for which modern analogues exist, and in ancient fossils preserved in a variety of sedimentary settings. The study of archaeological specimens provides important information on early diagenetic processes involving functionalized lipids, which are usually not evident in older specimens, especially those that have experienced more extreme thermal histories.

Analytical methods

Sampling

Fossil materials must be sampled with the aim of minimizing contamination from exogenous lipids. Plant organs may have been compressed during fossilization to a fraction of their original thickness, and it is necessary to avoid contaminating the specimen with the embedding sediment. Analyses of fossils removed by careful scraping from the sediment have yielded distinctive lipid distributions at concentrations consistent with modern counterparts (Lockheart *et al.* 2000). Particular care is required when sampling animal remains due to the potential for contamination of a specimen with lipids derived from human contact, which may be similar to those in the fossil (e.g. cholesterol and its derivatives).

Extraction and instrumental analysis

The analytical and instrumental techniques employed in the examination of lipids from fossils have their origins in biochemistry and organic geochemistry. Typically, lipids are extracted using high purity solvents, either by sonication or by using a Soxhlet apparatus for larger samples. Instrumental techniques such as gas chromatography (GC) and GC/mass spectrometry (GC/MS) are usually sufficiently sensitive to detect low concentrations of material and to quantify and identify biomarkers. Simultaneous analysis of all compound classes as a total lipid extract may be achieved by high-temperature GC (Evershed *et al.* 1995) but the complexity of some mixtures may obscure minor constituents. Further fractionation of lipids can be undertaken by solid phase extraction, thin layer or 'flash' column chromatography, to resolve minor components from the mixture. Compound-specific stable isotope measurements can be performed by GC/combustion/isotope ratio mass spectrometry (GC/C/IRMS). At present, only $^{13}C/^{12}C$ measurements (expressed as $\delta^{13}C$ values) have been carried out on fossil material but the possibility exists for the measurement of other isotopes, i.e. $^{18}O/^{16}O$ and D/H.

Lipid composition

Plants contain a wide range of biochemical components that serve protective, structural, or storage functions. Lower molecular weight lipids preserved include aliphatic compounds, such as *n*-alkanes, *n*-alkanols, fatty acids, long-chain ketones, wax esters, and oxygenated alkyl compounds (Table 3.1.3.1). Isoprenoid lipids which may also be preserved include sterols, triterpenoids, phytol, and others. Naturally polymerized structural lipids including cutan (polyalkyl), cutin, and suberin (polyester) are discussed in Section 3.1.5. Triacylglycerols exist primarily as energy stores (e.g. seed oils) but rarely survive intact due to their susceptibility to hydrolysis, free radical-induced oxidation and polymerization, and enzymatic β-oxidation (Fig. 3.1.3.1).

The major lipids biosynthesized by animals serve either protective (waxes), structural (phospholipids and cholesterol), or storage (triacylglycerols) functions. Like those in plants, the waxes produced by animals comprise various long-chain alkyl components, including hydrocarbons and fatty acyl esters, and oxygenated components including sterols.

Indicators of decay and preservational processes

General

The hydrophobic nature of many lipids limits their loss to porewater from the immediate vicinity of a fossil. However, all lipids can be degraded by saprotrophic organisms and are consumed at least until the local environment becomes nutrient limited or hostile to biological activity. The development of substantial populations of microorganisms during decay may result in the introduction of a microbial lipid signature superimposed on those endogenous to the fossil. In addition, lipids associated with particulate matter adhering to fossil tissues may be transferred as a result of compression or physicochemical processes.

Animals

Microbes are the major degraders of lipids in fossil animal remains (Fig. 3.1.3.1). Marker compounds such as hopanoids are indicative of the activity of saprotrophic bacteria which may be of exogenous or endogenous origin. For example, bones from archaeological sites have been shown to contain diploptene [hop-22(29)-ene] which derives from their invasion by aerobic bacteria (Evershed *et al.* 1995) (Fig. 3.1.3.1). Studies of numerous specimens of animal bone in a similarly good preservational state rarely, if ever, show acylglycerol lipids (e.g. triacylglycerols and phospholipids) in appreciable quantities, even though these are the major lipid components of the bones of extant mammals. This lack of acylglycerol lipids is further evidence of the activities of degradative organisms such as bacteria. Hydrolysis of acyl lipids yields fatty acids which are readily consumed by microorganisms. Most vertebrates and invertebrates also contain populations of symbiotic microorganisms. For example, the significant quantities of coprostanol in the tissues of a bog body (see Section 3.3.8) must have been produced by the activities of

endogenous enterohepatic bacteria invading the tissues postmortem.

Chemical degradation becomes more significant once microbial activity has ceased. The presence of 7-oxocholesterol in subfossil animal bones provides clear evidence of chemical degradation reactions mediated by free oxygen, probably via its singlet state. Free radical oxidation of unsaturated lipids also occurs in desiccated human mummies, as indicated by the presence of complex mixtures of monohydroxy and dihydroxy fatty acids and dicarboxylic acids (Buckley *et al.* 1999). The formation of an aliphatic polymer during diagenesis in invertebrate cuticles of Mesozoic and Palaeozoic age is presumed to arise via polymerization of lower molecular weight lipids (Stankiewicz *et al.* 1997).

Plants

Fossil remains from the sedimentary sequence of the Miocene lake bed at Clarkia, Idaho, USA have yielded alkyl lipids derived from epicuticular waxes which have distinctive distributions and abundances considerably higher than the enclosing sediments (Lockheart *et al.* 2000). However, concentrations of these simple compound classes in Clarkia fossils are lower than in their extant relatives, suggesting a limited degree of degradation, most likely via β-oxidation. Esterified components such as wax esters have been hydrolytically cleaved and contribute long-chain fatty acids and *n*-alkanols to the free lipid profile. The Clarkia fossils also contain series of ω-hydroxy acids and α,ω-diacids at low concentrations which most likely derive from the breakdown of the plant biopolymer cutin (Huang *et al.* 1996 and references therein).

Polyisoprenoidal compounds serve as more specific markers for particular taxa. For instance, diagenetically modified diterpenoid compounds with an abietane type carbon skeleton are characteristic of conifers. Microbial reprocessing of plant-derived triterpenoids is evident in the macrofossil remains at Clarkia from the progressive aromatization of these compounds and the occurrence of A ring-cleaved forms (Logan and Eglinton 1994). The presence of hopanoids in the sediments further underlines the importance of bacterial activity in influencing the final preserved lipid signature.

Palaeoenvironmental and palaeobiological information

Depositional environment

Lipids present in fossil remains can provide information on the conditions of preservation both before and after deposition. The presence of the cholesterol oxidation product, 7-oxocholesterol, in animal bones is indicative of a burial environment where oxygen was freely available. In lacustrine sedimentary environments hopanoids provide evidence for the activities of bacteria. It is difficult to determine when the bacteria were active as such compounds may derive from either bacterial populations active on the senescent or decaying leaf, or those that became associated with the leaf during burial. 3β-Methylated hopanoids are the only markers for a specific class of bacteria associated with leaf fossils. They are produced by sedimentary or water-column bacteria that use methane as a carbon source under anoxic conditions (methanotrophs). The $\delta^{13}C$ values of hopanoids contributed by organisms living under different conditions and from different levels in the water column/sediment will reflect the carbon source used.

Why fossils and their associated lipids are well preserved at some sites and not others has yet to be fully defined. Rapid deposition and burial of biological tissues increase their preservation potential, as do anoxic conditions which exclude macrofaunal grazing. Natural toxins, such as tannins in leaves, may also limit the extent of bacterial degradation.

Palaeoenvironmental applications

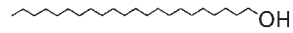
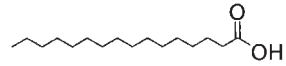
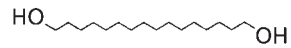
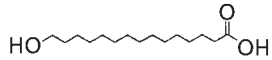
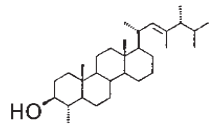
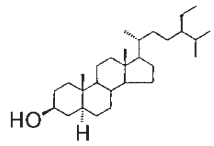
Plants adapt to local environmental conditions, such as water availability and light levels. Such adaptation affects isotope fractionation during CO_2 assimilation, and consequently the isotope composition of preserved biosynthetic products records palaeoenvironmental conditions. For example, lipids synthesized by a plant growing with an adequate supply of water have a lower ^{13}C content than those of a plant growing under water stress. In addition, the $\delta^{13}C$ values of individual lipids from fossil leaves preserve the isotope composition of the primary CO_2. Hence, the potential exists for the use of lipid $\delta^{13}C$ values, in conjunction with $\delta^{13}C$ values of other preserved biomolecules (e.g. lignin and cellulose), as a proxy for $\delta^{13}C$ of palaeoatmospheric CO_2.

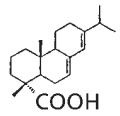
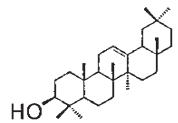
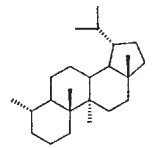
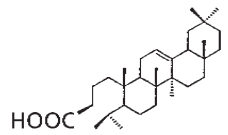
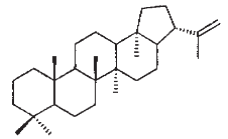
Palaeobiological information

Where depositional conditions favour the preservation of lipids, their distribution and stable isotope composition may be exploited for chemotaxonomic purposes. For example, *n*-alkanes and *n*-alkanols derived from leaf waxes in fossil specimens of *Magnolia*, *Quercus*, *Platanus*, *Pseudofagus*, and several coniferous genera from Clarkia show consistent differences in their distribution patterns. Furthermore, chemotaxonomic similarities in the lipid profiles of fossil *Quercus* specimens and certain modern species of oak were sufficient to assign the fossils to the 'red' subgenus of *Quercus*, reinforcing their morphological assignment (Lockheart *et al.* 2000). Other compound classes are too widespread between families

Table 3.1.3.1 Summary of lipid compound classes found in association with macrofossil remains.

PART 1

Lipid class	Biological origin	Route of formation (i.e. direct input or degradation process)	Examples	Example structures	Application or utility
***n*-Alkyl lipids**					
n-Alkanes	Epicuticular waxes of higher plants, invertebrate waxes	Direct input	C_{25} to C_{33} *n*-alkanes with odd/even predominance	C_{25} *n*-alkane	Chemosystematics of different fossil genera using distribution patterns
n-Alkanols	Plants and algae	Direct input or hydrolytic degradation of wax esters	C_{22} to C_{32} *n*-alkanols with odd/even predominance	 C_{22} *n*-alkanol	Lake productivity indicator?
Fatty acids	Plants, animals, bacteria	Direct input or hydrolysis of triacylglycerols and phospholipids	Bimodal distribution; 16:0 and 18:0 fatty acids from microbes; 20:0 to 34:0 fatty acids with even/odd predominance from plant waxes	 16:0 fatty acid	May indicate the action of saprotrophic organisms, e.g. in bones. Gram-positive bacteria produce iso- and antiso-branched acids
α,ω-Diols, ω-hydroxy acids	Plants	Breakdown of cutin and suberin biopolymers	16:0, 18:0 ω-hydroxy acids, Clarkia, USA	 C_{16} α,ω-diol  C_{16} ω-hydroxy acid	Shows the presence of biopolymeric remains which have been either partially or fully degraded
Polyisoprenoids					
Steroids	Algae, higher plants, animals	Direct input; oxidized/reduced by microbial activity or chemical reaction in the sediments	Dinosterol—dinoflagellate algae Stigmastanol—reduction of sitosterol (plants) 7-oxocholesterol—chemical oxidation of cholesterol, e.g. bones	 Dinosterol  5α-Stigmastan-3β-ol	Marker compounds for specific organisms Functional moieties present will give an indication of diagenetic conditions within the sediment

Compound class/ compound	Biological origin	Route of formation (i.e. direct input or degradation process)	Examples	Example structures	Application or utility
Diterpenoids	Conifer resins and essential plant oils	Direct input or diagenetically modified	Phyllocladane, abietic acid (Weisselster basin, Germany)	 Abietic acid	Gymnosperm biomarkers
Triterpenoids	Algae, higher plants		β-Amyrin, lupane	 β-Amyrin	Higher plant biomarkers
Des-A-triterpenoids	Higher plants	Microbially mediated loss of triterpenoid A ring	Des-A-lupane, Clarkia, USA	 Des-A-lupane	Sedimentary conditions and maturity of site
Seco triterpenoids	Higher plants	Predepositional photochemical reaction or microbial oxidation	3,4-Seco-olean-12-en-3-oic acid	 3,4-Seco-olean-12-en-3-oic acid	Sedimentary conditions and maturity of site
Hopanoids	Bacteria (and some ferns)	Direct input or diagenetic transformation	Diploptene [hop-22(29)-ene]—aerobic bacteria; 3-methyl hopanoids produced by methanotrophic bacteria	 Diploptene	Indicators for different bacterial communities Stereoconfiguration at 17 and 21 positions is related to the thermal history of sediment

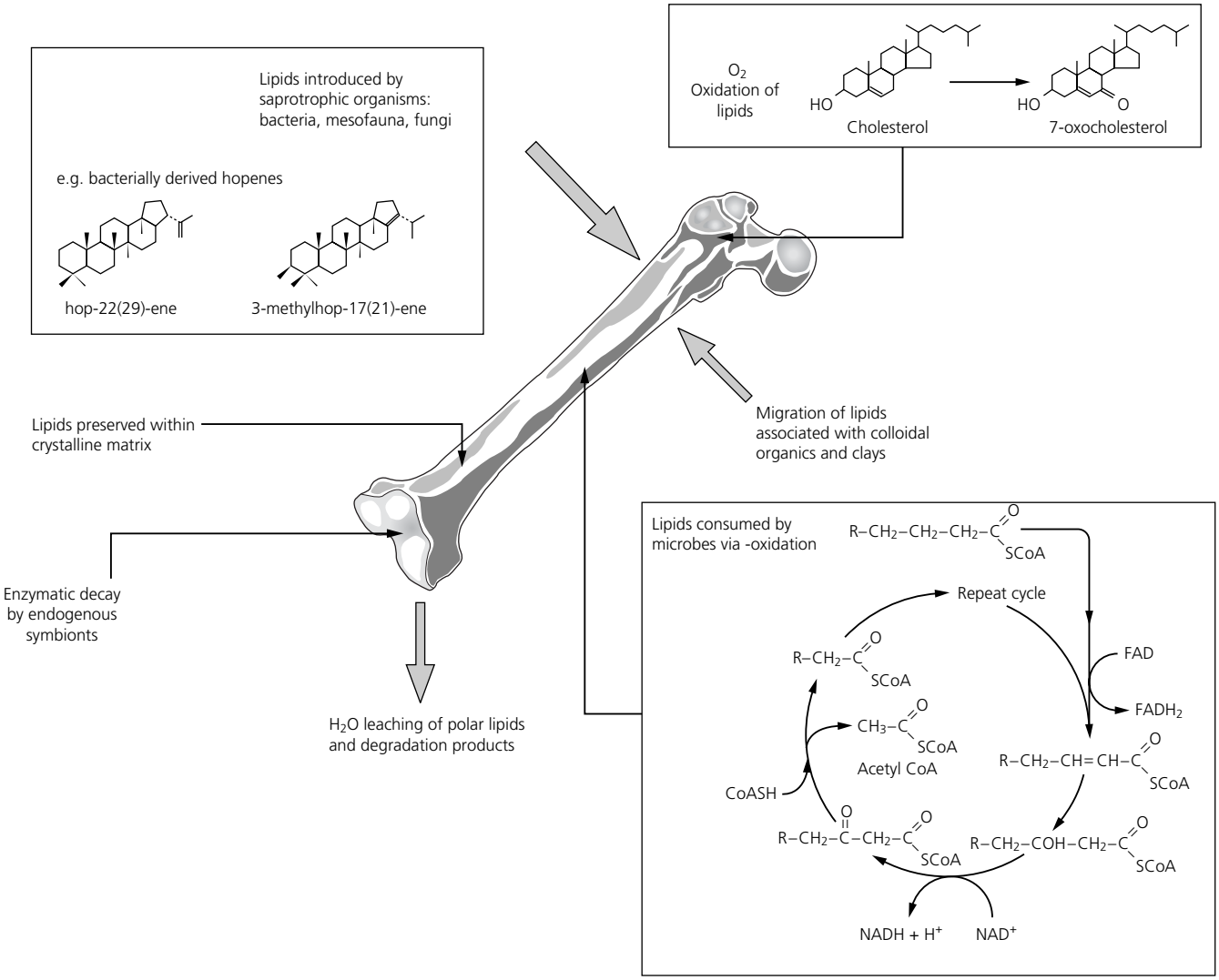


Fig. 3.1.3.1 Decay and diagenetic processes which affect lipids within buried biological material. Endogenous lipids may be modified by chemical reactions or microbial activity while exogenous lipids may also be introduced from invading organisms or from the surrounding sediment.

to be chemotaxonomically useful (e.g. diterpenoids derived from gymnosperms).

Lipids have attracted less attention as chemotaxonomic markers in the animal kingdom, although some modern invertebrates have been investigated. Cuticular hydrocarbons have been used to distinguish between different species of insect. However, the poor preservation potential of many invertebrates, and the relatively small size of fossil specimens, may limit their suitability for chemotaxonomic techniques.

Compound-specific carbon isotope analysis by GC/C/IRMS may allow the metabolic group to which an extinct species of plant belonged to be identified on the basis of differences in $\delta^{13}C$ values of compounds synthesized in plants utilizing different photosynthetic pathways, i.e. Calvin (C_3), Hatch–Slack (C_4), or crassulacean acid metabolism (CAM) pathways. Measurement of stable isotope ratios of fossil animal-derived cholesterol may be combined with those of collagen and individual amino acids for palaeodietary reconstruction and provide an indication of the trophic status of the animal within a food chain.

References

Buckley, S.A., Stott, A.W. and Evershed, R.P. (1999) Studies of organic residues from ancient Egyptian mummies using high temperature gas chromatography–mass spectrometry and

sequential thermal desorption gas chromatography–mass spectrometry and pyrolysis gas chromatography–mass spectrometry. *Analyst* **124**, 443–452.
Evershed, R.P., Turner-Walker, G., Hedges, R.E.M., Tuross, N. and Leyden, A. (1995) Preliminary results for the analysis of lipids in ancient bone. *Journal of Archaeological Science* **22**, 277–290.
Huang, Y., Lockheart, M.J., Logan, G.A. and Eglinton, G. (1996) Isotope and molecular evidence for the diverse origins of carboxylic acids in leaf fossils and sediments from the Miocene Lake Clarkia deposit, Idaho, U.S.A. *Organic Geochemistry* **24**, 289–299.
Lockheart, M.J., van Bergen, P.F. and Evershed, R.P. (2000) Chemotaxonomic classification of fossil leaves from the Miocene Clarkia lake deposit, Idaho, USA, based on *n*-alkyl lipid distributions and principal component analyses. *Organic Geochemistry*, **31**, 1223–1246.
Logan, G.A. and Eglinton, G. (1994) Biogeochemistry of the Miocene lacustrine deposit at Clarkia, northern Idaho, USA. *Organic Geochemistry* **21**, 857–870.
Stankiewicz, B.A., Briggs, D.E.G. and Evershed, R.P. (1997) Chemical composition of Paleozoic and Mesozoic fossil invertebrate cuticles as revealed by pyrolysis gas chromatography mass spectrometry. *Energy and Fuels* **11**, 515–521.

3.1.4 Bacteria

K. LIEBIG

Introduction

Bacteria are the most successful organisms on Earth: they are the oldest life forms, they are ubiquitous, and without them our planet's ecosystems could not exist. Life on Earth is grouped into three domains: Bacteria, Archaea, and Eukarya (Woese *et al.* 1990). Bacteria and Archaea, equivalent to the former eubacteria and archaebacteria, are prokaryotes. Eukarya are single or multicellular organisms with membrane-bound nuclei. Here the term 'bacteria', with a small 'b', is used in the old sense and includes all prokaryotes.

In the search for the origin of life on Earth, fossil bacteria have been detected in a variety of Precambrian sediments. Reports of fossil bacteria in the Phanerozoic are scarce, but this probably reflects only a lack of scientific interest, as they occur in sediments such as phosphorites, freshwater limestones, and deep-sea siliceous oozes (Liebig 1998a). The discovery and investigation of such minute objects as fossil bacteria mainly relies on scanning and transmission electron microscopy (SEM and TEM).

Identifying fossil bacteria

Bacteria in the Phanerozoic record are usually preserved by lithification. Their original organic matter is partly or wholly replaced by minerals, such as apatite, calcite, silica, pyrite, or siderite (Liebig 1998a,b). Thus, fossil bacteria can be identified by their morphology, but their simple shape means that other criteria must be used to distinguish them from similar non-bacterial structures. Characteristic features of bacteria are their size and shape, cellular division, association, substrate-bound occurrence, and internal structure.

Size and shape

The size of most bacteria falls between 0.5 and 2 μm in diameter or length, although there are exceptions. Cyanobacteria and spirochaetes are commonly larger. The existence of so-called nanobacteria (0.05–0.4 μm) has been a controversial subject for some time. Recently they were discovered by O. Kajander (University of Kuopio, Finland) inside human cells and blood. Their lithification leads to the formation of kidney-stones and other illnesses involving mineral formation.

Bacteria are either spherical (cocci) or rod-shaped (bacilli). Other morphologies are variations of these two basic forms, such as oval or short rods (coccobacilli), fusiform bacilli or filaments, curved rods (vibrios) or spirals (spirilla and spirochaetes). Spherical forms may be arranged in irregular accumulations (staphylococci), in chains (streptococci), or in aggregates of two (diplococci), plates of four (tetracocci), or cubes of eight (sarcinae). Some bacilli may be club-shaped (coryneform) or may show thickened ends or middle parts when carrying spores.

Cellular division

Reproduction by cellular division is a characteristic of all bacteria; this feature may be preserved in the fossil record (Fig. 3.1.4.1e).

Association

Bacteria occur very rarely as isolated cells. Colonies rarely contain just one species; the more common multispecies colonies are known as consortia. Bacteria can build more complex structures known as biofilms, which grow on a variety of substrates and consist of a tough film of adhesive, extrapolymeric substances (EPS) secreted by bacteria. The biofilm may also contain other microorganisms, such as fungi or algae, as well as sediment particles and authigenic minerals (see also Section 3.2.4). Fossil bacteria are identified by their occurrence in consortia, where they display a mixture of morphologies

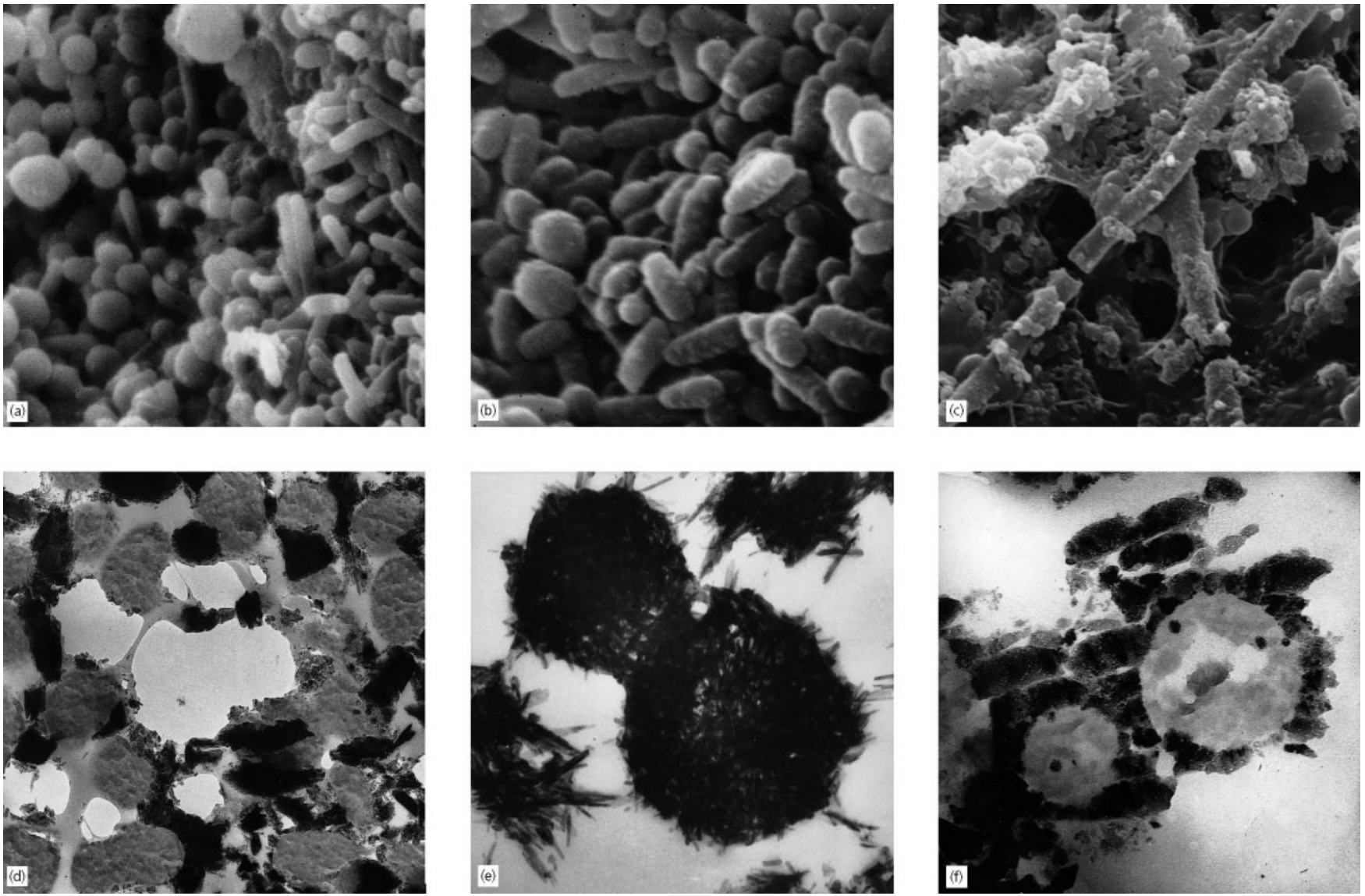


Fig. 3.1.4.1 SEM (a–c) and TEM (d–f) micrographs of fossil bacteria from Tertiary oil shales, Germany. (a) Phosphatized cocci and filamentous bacteria (0.5–1.5 µm) from the eye of the fish *Rhenanoperca* sp. (b) Calcified coccobacilli (0.5–1 µm) from the eye of a fish. (c) Fossil biofilm on wood, showing calcified fungal hyphae (1.3 µm in diameter) and bacteria embedded in spider-web-like calcified EPS. (d) Phosphatized bacterial casts (0.5 µm) within a scale of the fish *Atractosteus strausi*. (e) Dumbbell-shaped cast (1 µm long), probably representing cells in a state of division, from a coprolite; the mineral is an acicular apatite. (f) Cast-and-crust structures (0.4 and 0.7 µm) from a scale of *A. strausi*. (a,d–f) Messel; (b,c) Willershausen. (a,d–f, From Liebig 1998a.)

(Fig. 3.1.4.1a,b), or in biofilms (Fig. 3.1.4.1c). The structure of biofilms is as much a characteristic of fossil bacteria as the cells themselves. Spherical structures, the same size as bacteria, can be formed abiotically.

Substrate-bound occurrence

Extant bacteria prefer environments that favour microbial activities, and this should also be true for fossil bacteria.

Internal structure

Bacteria contain no membrane-bound organelles. TEM studies of lithified bacteria, whether fossilized or experimentally lithified, have so far failed to reveal any internal structures, except for possible former gaseous or liquid inclusions. However, such studies demonstrated that fossil bacteria may be preserved in various ways: as casts (Fig. 3.1.4.1d,e), crusts, cast-and-crust structures (Fig. 3.1.4.1f), moulds, and mould-and-cast structures (Liebig *et al.* 1996; Liebig 1998a). A cast represents just the lithified cytoplasm, when no cell wall is preserved. In contrast, a crust represents just the lithified cell wall. In a cast-and-crust structure, both the cell wall and the cytoplasm are preserved. A mould is the empty space in a mineral precipitate which indicates that bacteria were present during the precipitation process. A mould-and-cast structure is formed when a mould is later infilled by a mineral, or when a cast is later embedded in a mineral precipitate.

Taphonomy

The lithification of bacteria is not yet fully understood. It seems to depend on the species and especially on the structure of its cell wall; the process is most likely highly selective. As soon as a bacterium dies and metabolism stops, the cell is destroyed by autolytic processes. The preservation of bacteria requires either that such processes are slowed down significantly (or stopped altogether) so that there is time for mineral formation, or that mineralization occurs very rapidly (within hours).

The first step in the lithification of bacteria is an accumulation of metallic ions by the still living cell, either in or on the cell wall or inside the cytoplasm. The affinity of bacteria for metallic ions is well known and is widely used in mining processes. Even dead bacteria may continue to accumulate metallic ions (Beveridge and Doyle 1989). The incorporated metals (especially iron) inhibit autolysis in the dead cell by stabilizing the constituent wall polymers (Ferris *et al.* 1988).

Laboratory experiments have shown that the structure of the cell wall plays an important role in metal accumulation (Ferris *et al.* 1988; Westall 1997). These investigations have been carried out with Gram-positive and Gram-negative Bacteria. In the Archaea the cell walls differ from species to species; consequently no general statements can be made. A common feature in the cell walls of Bacteria is the peptidoglycan layer, which has a stabilizing function. Located between the inner and outer cell membrane, this layer is up to 40 times thicker in Gram-positive Bacteria than in Gram-negative Bacteria. In addition, Gram-negative Bacteria possess a complex outer membrane, whereas in Gram-positive Bacteria this membrane may consist only of some proteins or it may be totally absent. The peptidoglycan layer is associated with wall carbohydrates, such as teichoic acids, which contain highly negatively charged groups. These groups collect metallic ions from the surrounding water which act as nucleation sites for the formation of minerals. Gram-positive Bacteria are more prone to lithification because of their much thicker peptidoglycan layer. This has been confirmed by laboratory experiments (Ferris *et al.* 1988; Westall 1997).

Soft-tissue preservation of some macrofossils provides a special case of bacterial fossilization. An investigation of soft tissues from the Tertiary lacustrine oil shales of Messel, Rott, and Willershausen (Germany) showed that the labile organic material has been replaced in microscopic detail by layers of lithified bacteria (Liebig 1998b); even single hairs or the barbules of feathers can be distinguished (Liebig 1998a). Thus the exceptional preservation of macrofossils in certain Lagerstätten relies on the even more exceptional preservation of bacteria (Liebig 1998a,b).

Taxonomy

Recent bacteria are classified according to either their metabolism or their genetic relationships, but these features cannot be investigated in fossil bacteria. The morphology of Recent bacteria cannot be used to determine species. In addition, only a small percentage of Recent bacteria have yet been described. Consequently, it is very difficult to identify species of fossil bacteria. Nevertheless, some evidence may help to restrict the choice of possible species; for example, substrate type and the lithifying minerals may reflect the original environment and the metabolism of the bacteria when alive. In the case of Messel (Liebig 1998a), the fossil bacteria are autochthonous and embedded in euxinic sediments; evidently they were anaerobes or facultative anaerobes. They outline the former organic material in microscopic detail, which implies that they were heterotrophs. Laboratory experiments have shown that Gram-positive Bacteria lithify fairly readily. A group of anaerobic, heterotrophic and Gram-positive Bacteria are the Clostridia. In addition, Clostridia are known to be the main decomposers in anaerobic environments today.

Therefore, it is reasonable to suggest that the fossil bacteria in Messel belonged to the Clostridia (Liebig 1998a).

Future research

The preservation of bacteria is a more common phenomenon than is generally thought. Intensive studies of sediments that once favoured microbial life may reveal a plethora of lithified microorganisms and biofilm structures, especially in association with soft-tissue preservation. The elucidation of fossilization processes needs further interdisciplinary research, with the main emphasis being on laboratory experiments. Interest in this subject was boosted by the discovery of bacteria-like structures in the Martian meteorite ALH84001 in 1996 (see Section 1.1.2). A thorough knowledge of the character of such structures in terrestrial material will help to answer questions that arise during the search for traces of life in extraterrestrial material.

References

Beveridge, T.J. and Doyle, R.J., eds. (1989) *Metal ions and bacteria*. John Wiley, New York.

Ferris, F.G., Fyfe, W.S. and Beveridge, T.J. (1988) Metallic ion binding by *Bacillus subtilis*: implications for the fossilization of microorganisms. *Geology* **16**, 149–152.

Liebig, K. (1998a) Fossil microorganisms from the Eocene Messel Oil Shale of Southern Hesse, Germany. *Kaupia-Darmstädter Beiträge zur Naturgeschichte* **7**, 1–95.

Liebig, K. (1998b) Fossil bacteria and their role in soft-tissue preservation. Abstract. *Geoscience* **98**, 16.

Liebig, K., Westall, F. and Schmitz, M. (1996) A study of fossil microstructures from the Eocene Messel Formation using transmission electron microscopy. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **4**, 218–231.

Westall, F. (1997) Influence of cell wall composition on the fossilisation of bacteria and the implications for the search for early life forms. In: C.B. Cosmovici, S. Bowyer and D. Wertheimer, eds. *Astronomical and biochemical origins and the search for life in the Universe*, pp. 491–504. Editrici Compositori, Bologna.

Woese, C.R., Kandler, O. and Wheelis, M.L. (1990) Towards a natural system of organisms: proposal for the domains Archaea, Bacteria, and Eukarya. *Proceedings of the National Academy of Sciences USA* **87**, 4567–4597.

3.1.5 Resistant Plant Tissues — Cuticles and Propagules

P.F. van BERGEN

Introduction

Fossil plants are preserved in a number of different ways. These include impressions, permineralizations, and organically preserved structures (Jones and Rowe 1999). Most modern plants lack biomineralized tissues; hence their survival in the fossil record relies to a great extent on the preservation of organic remains. Abundant organic plant fossils include wood remains, pollen and spores, algae, leaves, and propagules. With the exception of wood, they are rarely preserved as complete plant organs but normally just as their resistant outer coverings (i.e. pollen and spore walls, algal cell walls, cuticle, seed coats, and fruit walls). The physical properties and chemical composition of plant structures vary, resulting in differences in their susceptibility to decay and in their behaviour during diagenesis. Those structures which are most resistant, either physically and/or chemically, have the highest organic fossilization potential. This inevitably produces a taphonomic bias in the fossil record, both within and between categories of plant organ/structure (Tegelaar *et al.* 1991; van Bergen *et al.* 1995).

Modern plant cuticles

One of the great innovations in land plants was the evolution of the cuticle (Edwards *et al. in* Cutler *et al.* 1982). This external layer covers all leaf and green stem surfaces. It serves a number of possible functions, including the reduction of water loss, the control of gaseous exchange, and the provision of a barrier to fungal pathogens (Baker *in* Cutler *et al.* 1982). The cuticle (*sensu lato*; see Holloway *in* Cutler *et al.* 1982) in modern plants is composed of a solvent-soluble wax fraction and an insoluble matrix (Tegelaar *et al.* 1991). The matrix makes up the framework of the cuticle and is composed of either a biopolyester, cutin, or an insoluble non-hydrolysable macromolecule, cutan, or (most commonly) a mixture of both. The chemical structure of cutin is reasonably well understood and is based primarily on functionalized C_{16} and C_{18} alkanoic acids (Tegelaar *et al.* 1991). In contrast, the precise structure of cutan is still unclear, but it appears to be based mainly on linear long-chain aliphatic compounds which are covalently bound via non-hydrolysable bonds. All three cuticular components (waxes, cutin, and cutan) are important to the

decay-resistant nature of leaves and stems. In addition, the cuticle may incorporate parts of the outer cell walls of the epidermis, which further contribute to its resistant properties.

Modern propagule walls

The walls of propagules (seed coats and fruit walls) are physically resistant outer envelopes which protect the labile genetic material inside. They are normally composed of various distinct layers, depending on the species. Many propagule walls contain a sclerotic (i.e. hardened, thickened) outer covering (sclerotesta or sclerotic endocarp) and a translucent inner layer (tegmen or translucent testa). In modern specimens these two distinct layers are firmly joined, whereas they are often easily separated in fossils.

The sclerotic layers are usually composed of a number of cell layers, some of which may be heavily sclerified (sclereids); in most cases these provide physical resistance. Chemical resistance is provided by the bulk of the sclerotic layers which are composed of insoluble macromolecular material, normally ligno-cellulose complexes (van Bergen *et al.* 1995). These complexes are similar to the rigid, highly resistant chemical constituents of wood (secondary xylem) in higher land plants. The propagule walls, like the wood, of different taxa are composed of three distinct types of lignin, that in: (1) gymnosperms, (2) dicotyledonous angiosperms, and (3) monocotyledonous angiosperms. Tannins may also be involved, providing additional chemical resistance (van Bergen *et al.* 1996).

Microscopic and chemical analyses of sub-Recent propagules have shown that the inner translucent layer is a cuticle (van Bergen *et al.* 1995). Although this layer has yet to be analysed in modern specimens, it is reasonable to assume that its nature and composition are similar.

Fossil cuticles and propagule walls

To understand why cuticles and propagule walls are preserved, it is important to study both their morphology and chemistry. Light microscopy, and scanning and transmission electron microscopy (SEM and TEM) reveal information about gross morphology and ultrastructure, which in turn can be related directly to chemical composition. A range of techniques, including spectroscopy, chemolysis, and pyrolysis, can be used to obtain detailed molecular data (van Bergen *et al.* 1995; Jones and Rowe 1999). Relatively young material, or specimens that have suffered very little overburden, provide the most meaningful chemical signals.

The protective function of both cuticle and propagule walls means that they must be physically and/or chemically resistant; consequently it is not surprising that they are preserved in the fossil record. However, in some cases physically resistant outer coverings fail to survive, even though it is clear from other evidence that the species was present in the past (van Bergen *et al.* 1996). Thus, physical resistance does not guarantee fossilization.

Cuticles

Microscopic analyses of fossil cuticles reveal that they were originally similar to their modern counterparts. Chemical studies have shown that, in some cases, wax components can still be recognized and there is evidence for cutin (Tegelaar *et al.* 1991). However, although cutin is the dominant constituent of most modern cuticles, fossil cuticles normally consist of macromolecule-based long-chain aliphatic compounds, termed cutan. Since there is very little evidence that cutin survives in fossil cuticles, it would appear that the fossil record is strongly biased towards taxa with cuticles containing significant amounts of cutan (Tegelaar *et al.* 1991). Indeed, the presence of this aliphatic molecule is considered to be the main reason why morphologically intact cuticles survive in the fossil record (Tegelaar *et al.* 1991). Not surprisingly, the discovery of cutan in fossil cuticles triggered a search to identify it in modern cuticles.

The search for cutan in modern cuticles was based on the idea that the fossil record of plant remains is the result of selective preservation of highly resistant biomacromolecules. However, it turns out that very few modern cuticles contain substantial amounts of cutan, and even where a modern cuticle is devoid of cutan, fossil cuticle of the same genus may consist of a highly aliphatic macromolecule (Collinson *et al.* 1998). This has led to the hypothesis of within-cuticle diagenetic stabilization of normally labile aliphatic constituents for the formation of these highly aliphatic macromolecules (Collinson *et al.* 1998). However, it is unlikely that stabilization of cutin plays a major part, as this would reveal a very distinct pyrolysis pattern: dominance of products with C_{16} and/or C_{18} chain length.

Propagule walls

The sclerotic propagule layers, which contain lignin (Fig. 3.1.5.1), remain morphologically intact but suffer major chemical alteration during diagenesis. Differences in the enclosing sediment also affect the overall chemical composition and ultimately the morphology (van Bergen *et al.* 1995). Less chemical alteration occurs in coarse-grained sediments than fine-grained sediments which have experienced the same burial history. Not all modern sclerotic propagule layers contain lignin, and

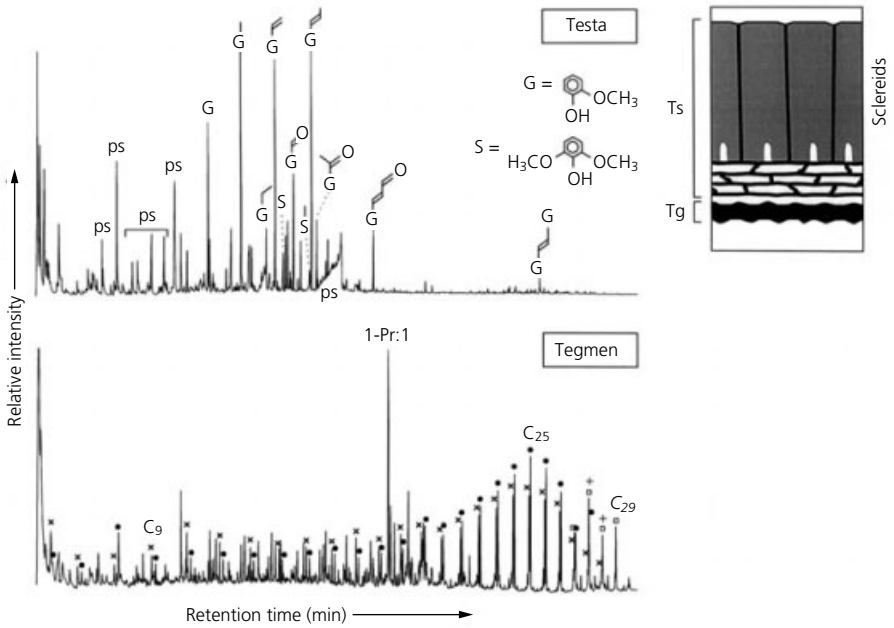


Fig. 3.1.5.1 Schematic representation of the seed coat of the sub-Recent water-lily *Brasenia schreberi* (Eemian interglacial) and pyrograms (Curie temp. 610°C) of the sclerotic lignin-containing outer layer (Ts, testa) and the translucent aliphatic inner layer (Tg, tegmen). ×, *n*-alk-1-enes; ●, *n*-alkanes; □, methylketones; ps, polysaccharide pyrolysis products; G and S, lignin markers; 1-Pr:1, prist-1-ene; C_{29}, 2-nonacosanone; C_{xx}, total carbon numbers for the alk-1-enes and alkanes; δ and γ, δ- and γ-tocopherols. See van Bergen *et al.* (1996) for additional information.

this has a major impact on their preservation potential. The sclerotic propagule wall of the Recent water-lily *Nelumbo*, for example, contains a polysaccharide–tannin complex and lacks lignin, in contrast to all fossil and most modern water-lily propagules. This lignin deficit may explain the absence of *Nelumbo* propagules in the fossil record, despite the exceptional longevity and ability to germinate, of the modern propagule (van Bergen *et al.* 1996).

The translucent inner layers of fossil propagules also contain aliphatic macromolecules based on long-chain components (Fig. 3.1.5.1). These cuticular layers in tegmen of fossil representatives of the modern water-lily *Brasenia*, ranging in age from approximately 100 Ka to 39 Ma, remain virtually intact during diagenesis, both microscopically and chemically (van Bergen *et al.* 1996). Furthermore, differences in the enclosing sediment do not obviously affect their chemical composition. Thus, regardless of whether the material was originally cutan or is a macromolecule formed during the early stages of diagenesis, the presence of long-chain aliphatic moieties allows these translucent propagule layers to be preserved.

Conclusion

Plant structures composed of both lignin and an aliphatic macromolecule are the most likely to be preserved in the fossil record (Fig. 3.1.5.2). However, the preservation potential of the aliphatic component itself is higher than that of lignin. For example, in the case of the seed coats of the cat's-tail *Typha*, cuticular layers containing an aliphatic macromolecule are selectively preserved, whereas thin-walled lignified layers are lost upon fossilization (van Bergen *et al.* 1995). Conversely, plant remains lacking both lignin and an aliphatic macromolecule are unlikely to be preserved as organic fossils (Fig. 3.1.5.2). The biases resulting from such differences must be considered when interpreting the fossil record.

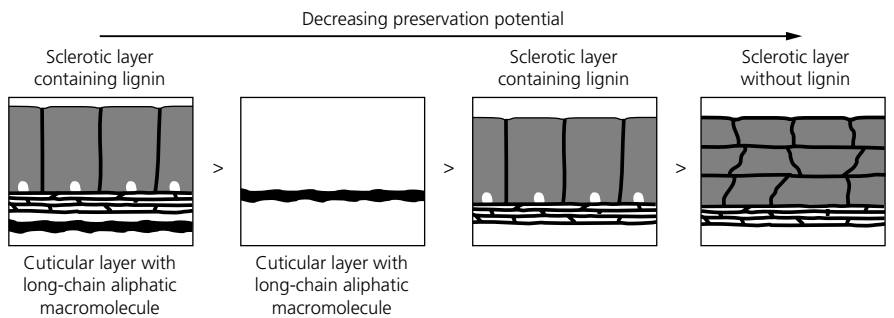


Fig. 3.1.5.2 Preservation potential of resistant plant tissues in the fossil record, related to chemical composition. Note that plant structures composed of both lignin and an aliphatic macromolecule have a higher preservation potential than structures solely containing either of these two molecules.

References

van Bergen, P.F., Collinson, M.E., Briggs, D.E.G., de Leeuw, J.W., Scott, A.C., Evershed, R.P. and Finch, P. (1995) Resistant biomacromolecules in the fossil record. *Acta Botanica Neerlandica* **44**, 319–342.

van Bergen, P.F., Collinson, M.E. and de Leeuw, J.W. (1996) Characterization of the insoluble constituents of propagule walls of fossil and extant water lilies: implications for the fossil record. *Ancient Biomolecules* **1**, 55–81.

Collinson, M.E., Mösle, B., Finch, P., Scott, A.C. and Wilson, R. (1998) The preservation of plant cuticle in the fossil record: a chemical and microscopical investigation. *Ancient Biomolecules* **2**, 251–265.

Cutler, D.F., Alvin, K.L. and Price, C.E., eds. (1982) *The plant cuticle*. Linnaean Society Symposium Series, no. 10. Academic Press, London.

Jones, T.P. and Rowe, N.P., eds. (1999) *Fossil plants and spores: modern techniques*. Geological Society, London.

Tegelaar, E.W., Kerp, J.H.F., Visscher, H., Schenck, P.A. and de Leeuw, J.W. (1991) Bias of the paleobotanical record as a consequence of variations in the chemical composition of higher vascular plant cuticles. *Paleobiology* **17**, 133–144.

3.1.6 Animal Cuticles

B.A. STANKIEWICZ and D.E.G. BRIGGS

Introduction

A number of invertebrates are protected by an outer layer known as the integument or cuticle (Neville 1993). The cuticle is connected to the internal muscles and protects the organism against predators; it provides a barrier to the environment and, in terrestrial forms, prevents dessication. In arthropods the cuticle consists of three major layers: the epicuticle, exocuticle, and endocuticle (Neville 1993). The outermost layer, the epicuticle, is only a few microns thick, whereas the combined thickness of the exocuticle and endocuticle is up to two orders of magnitude greater. Cuticles may be soft and flexible, or acquire a degree of stiffness and hardness that varies between taxa, and at different stages in their development (larva, pupa, or adult). The hardening of the cuticle involves either biomineralization (with calcium salts, e.g. some crabs and lobsters) or sclerotization (e.g. beetles, horseshoe crabs). The latter process, which is also called tanning, involves stabilization of proteinaceous moieties by reaction with quinones. The rigidity of the exoskeleton may increase through successive moults, as the old cuticle is shed and a new stronger cuticle is formed.

Cuticle chemistry and structure

The epicuticle consists of cuticular waxes, which are composed mainly of straight chain and branched hydrocarbons, wax esters, fatty acids, alcohols, ketones, and sterols (e.g. cholesterol), and function in preventing dehydration. The rest of the cuticle is composed mainly of two biopolymers, chitin and protein, which form a complex structure cross-linked by catechol, aspartic, and/or histidyl moieties (Briggs *et al.* 1998). Chitin, a nitrogen-containing polysaccharide, provides the structural strength of the cuticle, reinforced by the protein matrix. The components involved in cross-linking are more important in sclerotized cuticles; $CaCO_3$ seems to play a similar role in biomineralized cuticles, where it may be bonded to the organic biopolymers by weak chemical forces. The proportion of chitin to protein varies between taxa, ranging from just traces in Protozoa to up to 85% in some crustacean cuticles (Muzzarelli 1977). The preservation potential of chitin is higher than that of the associated proteins (Briggs *et al.* 1998; Stankiewicz *et al.* 1998a). However, almost all the estimated $\approx 10^{11}$ tonnes of chitin produced annually in the biosphere (most of it by arthropods) is consumed by decay, and only mineralized or sclerotized cuticles are normally preserved.

Investigations of the ultrastructure of arthropod cuticle, and its molecular organization, show that the chitin and proteins form microfibrils arranged in a plywood-like structure (Neville 1993). The development of new analytical techniques has led to the detailed chemical characterization of such cuticles, allowing their preservation history to be unravelled (Stankiewicz *et al.* 1998b; Briggs 1999). Pyrolysis-gas chromatography/mass spectrometry (Py-GC/MS) is particularly suitable for analysing the very small quantities ($\approx 100\,\mu g$) of recalcitrant macromolecular material that are often all that is available from fossil specimens. This method has been used to analyse and characterize many fossil and modern biological tissues, both plant (see Section 3.1.5) and animal. A combination of other techniques, such as Fourier transform infrared spectroscopy (FTIR), nuclear magnetic resonance (NMR), colorimetric assay, amino acid analysis, and high-performance liquid chromatography (HPLC), provides additional details of the fate of biopolymers in animal cuticles and their preservation in ancient sediments (Fig. 3.1.6.1) (Briggs *et al.* 1998). This is complemented by scanning and transmission electron microscopy, which reveal the degree to which the morphology of the fossil cuticle has been altered in parallel with changes in chemical composition. Such an approach relies on a comparison between the fossil arthropod and its living counterpart, and the assumption that the chemical composition of arthropod cuticles (i.e. the chitin–protein complex) has not changed significantly during their evolutionary history (Fig. 3.1.6.1).

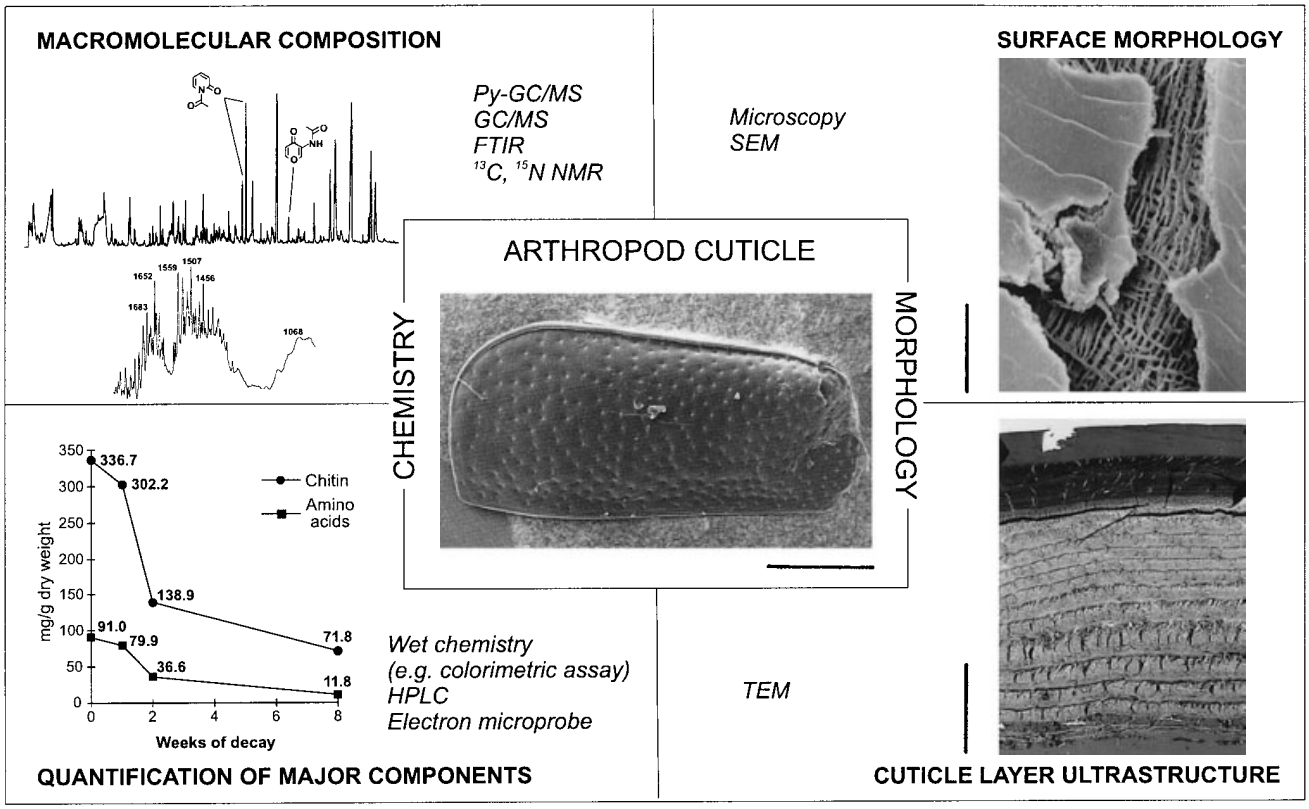


Fig. 3.1.6.1 Methods used in investigating the preservation of arthropod cuticle such as that of the wing case of a beetle from West Mabou, Nova Scotia (≈10 Ka; scale bar: 400 µm). Macromolecular composition may be analysed by a number of techniques (Py-GC/MS and FTIR traces are illustrated). Experiments reveal how the major components are affected by decay (e.g. laboratory decay of mantis shrimp cuticle for 8 weeks with a marine inoculum). Scanning electron microscopy (SEM) shows the surface and underlying chitinous fibres of the cuticle of a weevil from 3 Ma Lake Willershausen, Germany (scale bar: 20 µm). Transmission electron microscopy (TEM) shows a section through the cuticle of a Recent emperor scorpion (outer hyaline exocuticle, remaining exocuticle, and endocuticle; scale bar: 20 µm).

The preservation of fossil cuticles

Organically preserved animal cuticles are known from rocks as old as Cambrian (they occur in the Burgess Shale, for example, where they provide a template for the precipitation of clay minerals), and they are relatively common throughout the Palaeozoic (e.g. scorpions and eurypterids). The processes involved in degradation and diagenesis can be inferred on the basis of a comparison with Recent analogue species. Decay experiments have shown that the chitin component of the cuticle degrades even in anoxic conditions, but at a slower rate than the protein. Pleistocene asphalt seeps (e.g. Rancho La Brea in California) and organic-rich glacial deposits preserve abundant insect cuticles (Stankiewicz *et al.* 1998a). The proportion of chitin that survives reflects the nature of the sediment. Surprisingly perhaps, a consistently lower proportion of chitin is preserved in peat deposits than in more clastic sediments (Stankiewicz *et al.* 1998a). Acidic hydrolysis in peats may enhance the chemical degradation of the protein–chitin complex. A lithological control is also evident in the preservation of the cuticles of insects and freshwater shrimps from Pliocene (≈3 Ma) Lake Willershausen, Germany. Cuticles deposited in the oxygen-depleted waters of the lake bottom yield a much higher percentage of chitin than those near the lake margins. The oldest documented chitin survives in Oligocene (24.7 Ma) beetle cuticles, which also preserve traces of protein, from maar-type lake deposits at Enspel, Germany (Briggs *et al.* 1998). In each case where fossil cuticles reveal little chemical alteration, their structural details (i.e. chitinous fibrils) are also remarkably preserved. Cuticles preserved as inclusions in amber might be expected to be pristine. However, although they preserve the detailed external morphology, only younger (Pleistocene) resins (i.e. copal) show very good chemical preservation of insect cuticle; those extracted from 25 to 30 Ma Dominican amber are chemically changed (Briggs 1999).

Although organically preserved fossil cuticles appear

to be quite common in the terrestrial environment, and some, at least as old as Oligocene, retain a chitin–protein composition, similarly preserved cuticles of marine invertebrates are rare. Analysis of a diversity of cuticles from Tertiary marine crustaceans revealed no compelling evidence that the original chemistry is even partially preserved (Briggs *et al.* 1998; Stankiewicz *et al.* 1998a). This probably reflects the much more rapid biodegradation of cuticles in marine settings than in the terrestrial realm (Briggs 1999). Laboratory experiments also indicate that the heavily sclerotized cuticles of terrestrial organisms are more resistant to biodegradation than the organic components of the cuticles of marine arthropods, even where the latter are protected by biomineralization.

Palaeozoic and Mesozoic arthropod cuticles often show well-preserved surface details but they lack the helicoidal structure of the endocuticle (Neville 1993) which is characteristic of well-preserved Quaternary and some Tertiary fossils. Moreover, there is no trace of the chitin–protein component of the cuticle. Occasionally aromatic structures are present (Fig. 3.1.6.2) (Briggs *et al.* 1998), but the chemical composition of these cuticles usually shows a signature characteristic of aliphatic polymer. This aliphatic composition is believed to be the result of *in situ* polymerization of cuticular components during diagenesis (Fig. 3.1.6.2) (Stankiewicz *et al.* 1998b; Briggs 1999).

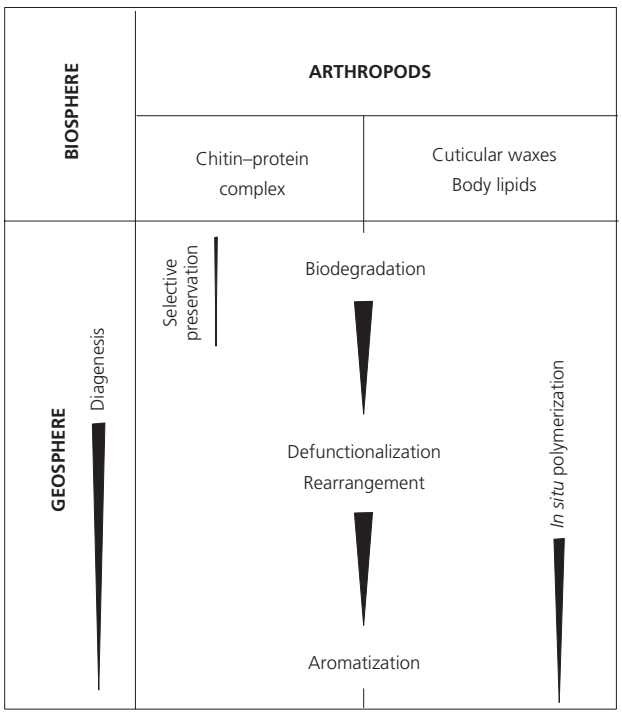


Fig. 3.1.6.2 The processes involved in the transfer of arthropod cuticles from the biosphere to the geosphere: the chitin–protein complex of the cuticle, and associated cuticular waxes and lipids, may be preserved by aromatization, or *in situ* polymerization to aliphatic biopolymer, *following* selective preservation.

Conclusions

The extent of chemical and structural degradation of arthropod cuticles, and their subsequent survival into the fossil record, depends on the following factors: (1) the type of organism (e.g. thickness of cuticle; degree of sclerotization or biomineralization); (2) the nature of the depositional environment (e.g. terrestrial or marine; climate; oxic or anoxic water and sediment; pH; organic productivity; rate of sedimentation); and (3) inhibition of microbial decay and subsequent diagenetic alteration (which is accelerated by elevated temperature and may be, to a degree, time dependent).

Cuticles provide an important key to the fate of organic matter in ancient sediments (i.e. kerogens). The aliphatic composition of the majority of fossil arthropod cuticles does not reflect the chitin–protein complex that makes up the cuticle of the living organism. Thus the fossilization of fossil arthropod cuticles cannot be attributed simply to selective preservation of their more decay-resistant components. Long-term preservation relies on the diagenetic polymerization of the cuticle to an aliphatic hydrocarbon (Stankiewicz *et al.* 1998b). Such a transformation may affect not only animal but also plant cuticles (see Section 3.1.5), and may be fundamental to the formation of certain types of kerogen (Briggs 1999).

References

Briggs, D.E.G. (1999) Molecular taphonomy of animal and plant cuticles: selective preservation and diagenesis. *Philosophical Transactions of the Royal Society of London B* **354**, 7–17.

Briggs, D.E.G., Evershed, R.P. and Stankiewicz, B.A. (1998) The molecular preservation of fossil arthropod cuticles. *Ancient Biomolecules* **2**, 135–146.

Muzzarelli, R.A.A. (1977) *Chitin*. Pergamon Press, New York.

Neville, A.C. (1993) *Biology of fibrous composites*. Cambridge University Press, Cambridge.

Stankiewicz, B.A., Briggs, D.E.G., Evershed, R.P., Miller, R.F. and Bierstedt, A. (1998a) The fate of chitin in Quaternary and Tertiary strata. In: B.A. Stankiewicz and P.F. van Bergen, eds. *Nitrogen-containing macromolecules in the biosphere and geosphere*, pp. 211–225. American Chemical Society Symposium Series No. 707.

Stankiewicz, B.A., Scott, A.C., Collinson, M.E., Finch, P., Mosle, B., Briggs, D.E.G. and Evershed, R.P. (1998b) The molecular taphonomy of arthropod and plant cuticles from the Carboniferous of North America. *Journal of the Geological Society* **155**, 453–462.

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3.1.7 Shells

K.H. MELDAHL

Introduction

By far the most common marine benthic macroinvertebrate remains in the fossil record are shells composed of calcium carbonate. Brachiopods were the dominant shell producers of the Palaeozoic, while mollusc shells dominate the post-Palaeozoic record. Mollusc shells have been the subject of the greatest number of taphonomic studies of any taxonomic group.

Shell destruction and alteration

Disarticulation

The separation of the two valves of bivalved shells (molluscs and brachiopods) occurs when connective ligaments and muscles decay. (In terebratulid and rhynchonellid brachiopods the hinge mechanism must also break for the valves to separate.) The rate at which disarticulation occurs depends on how robust the connective tissues are, and the nature of the decay environment. In general, decay is slower under anaerobic conditions and at lower temperatures. Bioturbation, scavenging, and physical turbulence accelerate disarticulation. Experiments show that disarticulation rates are highly variable, generally ranging from a few days to several months, depending on taxon and environment.

Abrasion and fragmentation

Shells may be physically ground down by sediment particles or other shells. Abrasion results in loss of shell mass, reduction of surface relief, and smoothing and rounding of shell features. The longer shells are exposed at the sediment surface, and/or the more turbulent the environment, the more pervasive is abrasion. Fragmentation may result from physical impact by particles, but is far more commonly due to biological activities like predation, scavenging, and bioturbation.

Bioerosion

The destruction of shell material by biological action is pervasive in most marine environments (see Section 3.2.2). Microboring algae and fungi, clionid sponges, and grazing gastropods (which rasp algal coatings off shells using their radulae) are the principal agents of shell bioerosion. Where shells are exposed continuously at the sediment surface, bioerosion rates exceeding 20% shell mass lost per year have been observed in modern marine environments. Without high magnification the effects of microbial bioerosion are indistinguishable from those of dissolution.

Dissolution and diagenesis

Dissolution of shell carbonate may occur at the sea floor, within shallow burial, or long after burial and lithification. In general, dissolution on or near the sea floor proceeds more rapidly where acidity increases due to organic decomposition (carbonic acid, H_2CO_3; nitric acid, HNO_3; phosphoric acid, H_3PO_4) and sulphide oxidation (sulphuric acid, H_2SO_4). Bioturbation enhances dissolution by mixing fresh sea water into the sediment. Shells with an organic-rich matrix appear to be more vulnerable to dissolution, in part because the matrix provides nutrients for microborers.

Most shell carbonates are either calcite (articulate brachiopods and a few bivalves) or aragonite (nearly all molluscs). Aragonite is distinctly less stable in diagenesis. In most rocks older than Pliocene age, aragonite shells have either dissolved away wholesale (usually leaving behind internal and external moulds) or have been partially or completely replaced by calcite or dolomite. Replacement usually causes loss of morphological detail, though more prominent shell features such as ridges, spines, or distinctive growth bands may be preserved. Shells composed of original calcite are often well preserved, though some may be recrystallized or dolomitized. Colour pigments in calcite or aragonite shells are almost never preserved.

Shell assemblages

Most recent work on shell taphonomy has focused on four major topics: (1) correspondence between live community and fossil assemblage; (2) use of shells as environmental and stratigraphic indicators; (3) rates of taphonomic alteration; and (4) time-averaging.

Correspondence between live community and fossil assemblage

How accurately is the composition and structure of an original community of shelled benthos reflected in its fossilized remains? A classic approach to this question has been to census living molluscan species and compare them to the dead shells accumulating in the same environment. Numerous investigations of this kind have demonstrated that, in general, dead shell assemblages closely reflect the skeleton-bearing component of original living communities (see review by Kidwell and Flessa 1995; also Section 3.3.1). It was once assumed that transportation of dead shells severely biased fossil

assemblages. Studies have now shown that dead shells of transported species are generally rare, and when present in a shell assemblage are typically derived from immediately adjacent habitats. Long-distance transport is rare. Repeated census of living communities over several years often improves the correspondence between the live species present and their dead remains, as rare and ephemeral species, initially represented only by dead shells, are eventually found alive. Dead shell assemblages are often accurate records of the long-term composition of live communities. This has great significance for palaeobiology, showing that ordinary shelly fossil assemblages may be used to address important questions regarding the structure and evolution of ancient communities.

Shells as environmental and stratigraphic indicators

Environmental processes alter shell remains in distinctive ways, yielding valuable information about ancient sedimentary environments. There is a vast literature documenting the taphonomic signatures produced by variation in wave and current energy, substrate, light, sedimentation, biological activities, water chemistry, and other environmental factors. Much of this work has been conducted in Holocene sedimentary environments, where the relationship between environmental process and resulting taphonomic signature can be directly documented (see reviews by Powell *et al.* 1989 and Parsons and Brett 1991). While most work to date has focused on shallow marine settings, and on time scales of 1–2 years, there is presently a strong push to extend both the time scale and the scope of sedimentary environments over which Holocene taphonomic data are collected. Taphonomic data are now commonly used to complement traditional stratigraphic and faunal approaches to palaeoenvironmental interpretation.

Sedimentary beds consisting of relatively dense accumulations of shells provide important information about stratigraphic patterns and processes. Such shell concentrations in the stratigraphic record frequently represent prolonged periods of low net sediment input and/or erosional scouring, during which dense accumulations of shells build up on the sea floor (Kidwell 1991). In some cases, shell-rich beds record rapid episodes of concentration, such as winnowing during storms. Shell concentrations are thus useful clues to the dynamics of sediment accumulation, to palaeoenvironmental interpretation, and to the identification of stratigraphic discontinuities.

Rates of taphonomic alteration

Most taphonomic processes other than diagenesis have their greatest effect at and immediately below the sediment–water interface, in the *taphonomically active zone* (TAZ; Powell *et al.* 1989). Shells might be expected to become increasingly altered the longer they spend in the TAZ. However, studies in Holocene environments have demonstrated a weak relationship between shell age in the TAZ and taphonomic condition (e.g. Meldahl *et al.* 1997). For example, Fig. 3.1.7.1 shows the relationship between radiocarbon age and taphonomic condition for more than 100 bivalve shells collected from the sediment surface in five different Holocene shallow marine sedimentary environments. The shells are grouped according to their degree of taphonomic alteration, from unaltered or minimally altered Grade 1 shells to extensively altered Grade 4 shells. No matter what the sedimentary environment, nearly all Grade 1, 2, and 3 shells are young (most are indistinguishable from 'modern' using radiocarbon dating) whereas Grade 4 shells range from 'modern' to several thousand years old (Fig. 3.1.7.1). The data demonstrate only an increase in shell *age variance* with increasing taphonomic alteration, and this happens only at the most advanced (Grade 4) stage of alteration. Since shell alteration rates are most rapid while shells are exposed at the sediment surface, and slow down while shells are in shallow burial, the weak relationship between shell age and taphonomic condition is likely due to the random manner in which shells are buried and exhumed by reworking in the TAZ.

Time-averaging

When old shells survive postmortem destruction and accumulate along with younger shells, the resulting shell assemblages are time-averaged. Since time-averaging sets limits on time resolution in palaeontological studies, there is great interest in understanding how much time is represented in fossil assemblages. Mollusc shells, since they are both important in the fossil record and amenable to age-dating in the Holocene (primarily using radiocarbon), have been the subject of several studies of time-averaging. Holocene molluscan assemblages are time-averaged over several orders of magnitude, depending on environment. Deeper shelf assemblages can represent more than 10 000 years. Nearshore shelf assemblages are typically time-averaged on the order of 1000 years. High sedimentation (rift basin) assemblages may represent only several hundred years (Flessa and Kowalewski 1994; Meldahl *et al.* 1997). These results provide some general guidelines for the duration of time-averaging that palaeontologists can expect in certain palaeoenvironmental settings. (See Section 3.2.7 for a detailed review of time-averaging.)

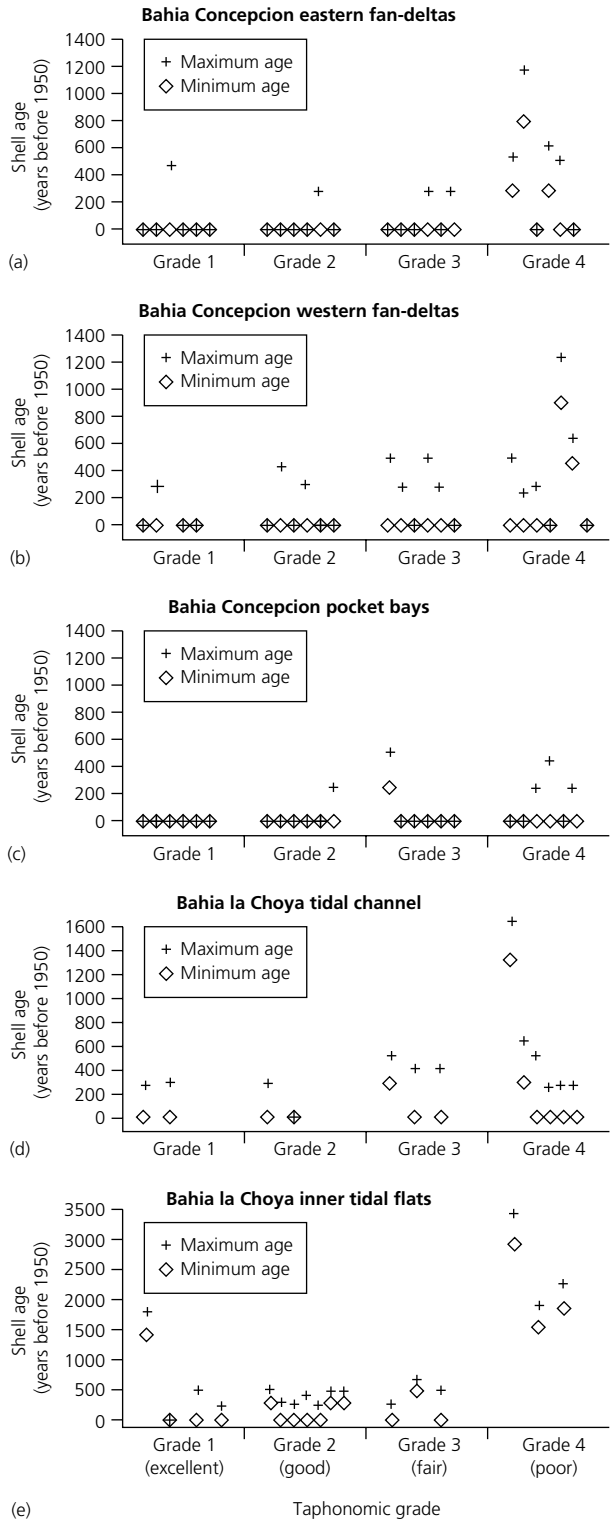

Fig. 3.1.7.1 Relationship between the radiocarbon calendar age of dead bivalve shells and their taphonomic condition in five (a–e) shallow marine sedimentary environments, Gulf of California, Mexico. Environments represented are two types of fan-deltas (a,b), sheltered carbonate pocket bays (c), tidal channel (d), and inner tidal flats (e). All shells were collected from the sediment surface and classified into one of four taphonomic grades: Grade 1, excellent preservation (no or minimal alteration); Grade 2, good preservation (slight alteration); Grade 3, fair preservation (moderate alteration); Grade 4, poor preservation (extensive alteration). Vertically paired maximum and minimum age data points represent 99% confidence interval on calendar age for each shell. Position of a shell along the horizontal axis within each grade is arbitrary. (From Meldahl *et al.* 1997; by permission of the Paleontological Society.)

References

Flessa, K.W. and Kowalewski, M. (1994) Shell survival and time-averaging in nearshore and shelf environments: estimates from the radiocarbon literature. *Lethaia* **27**, 153–165.

Kidwell, S.M. (1991) The stratigraphy of shell concentrations. In: P.A. Allison and D.E.G. Briggs, eds. *Taphonomy: releasing the data locked in the fossil record*, pp. 211–290. Plenum Press, New York.

Kidwell, S.M. and Flessa, K.W. (1995) The quality of the fossil record: populations, species and communities. *Annual Review of Ecology and Systematics* **26**, 269–299.

Meldahl, K.H., Flessa, K.W. and Cutler, A.H. (1997) Time-averaging and postmortem skeletal survival in benthic fossil assemblages: quantitative comparisons among Holocene environments. *Paleobiology* **23**, 207–229.

Parsons, K.M. and Brett, C.E. (1991) Taphonomic processes and biases in modern marine environments: an actualistic perspective on fossil assemblage preservation. In: S.K. Donovan, ed. *The processes of fossilization*, pp. 22–65. Columbia University Press, New York.

Powell, E.N., Staff, G., Davies, D.J. and Callendar, W.R. (1989) Macrobenthic death assemblages in modern marine environments: formation, interpretation and application. *Critical Reviews in Aquatic Science* **1**, 555–589.

3.1.8 Bones

C. DENYS

Introduction

Bone is found in nearly all vertebrates. It is characterized by a highly mineralized phase consisting mainly of hydroxyapatite, which gives hardness and resistance to compression forces. Bone also contains water (30%) and organic compounds, dominantly collagen, which provide elasticity and resistance to tensional forces. The

bones of all vertebrates are similar in structure and composition, allowing a common approach to their taphonomic study. The balance between the processes of destruction and preservation depends on the taphonomic history of each site where bones are concentrated or dispersed. Two main phases can be distinguished: before and after burial. During fossilization, bones are subjected to various modifications that alter their surface morphology, their structure and composition (Fig. 3.1.8.1). One of the aims of taphonomy is to identify these alterations, and the biases that result, in both faunal and skeletal representation in the bone assemblage.

Predation

Predation is the most common initial cause of modification of both large and small vertebrates. It causes characteristic marks on bone surfaces, e.g. tooth scratches, punctures, gnawing marks, and fracturing. When small vertebrates are totally ingested by a predator (e.g. owl, eagle, mammalian carnivore, crocodile), the passage through the digestive tract leaves very characteristic patterns of alteration on the surface of bones and teeth (Fig. 3.1.8.2). Five categories of digestion are recognized, as functions of both intensity (grades of digestion) and the frequency of digested elements (Andrews 1990) (Table 3.1.8.1). When the proportions and degree of breakage of the elements of the skeleton are added to the effects of digestion, five main categories of predator modification can be identified, from least (category 1) to most destructive (category 5) (Table 3.1.8.2). Fragmentation results from ingestion by a predator, and subsequent digestion enlarges osteoblasts on the epiphyses and produces a polished surface. Bones can be greatly damaged during digestion, yet still survive to become fossilized, and material processed by different predators can be mixed in the same accumulation (Fernandez-Jalvo *et al.* 1998). Digestion alters bone tissues chemically, causing a decrease in the Ca/P ratio (Fig. 3.1.8.3) and great variability in minor elements (Sr, Mg, Fe, Zn, Si, Al, Ba, Na) depending on the skeletal tissue considered and the nature and provenance of the predator (Dauphin *et al.* 1997).

Other factors

Other factors, which may have an influence before or after burial, also leave characteristic traces on bone surfaces (Fig. 3.1.8.4). Gradual fragmentation (by cracking, exfoliation, flaking), as a result of weathering, can lead to total destruction of the skeletons of both small and large mammals (Andrews 1990) in some environments. Other reported effects of weathering include an increase in

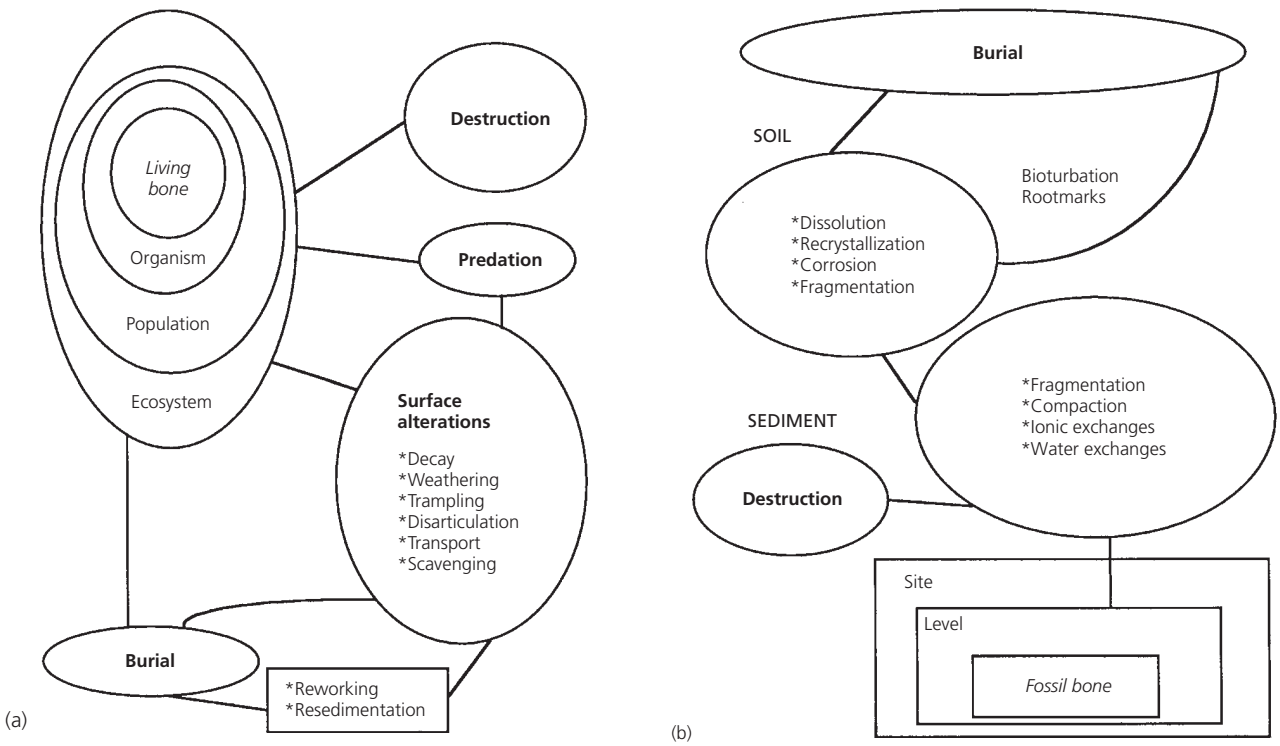

Fig. 3.1.8.1 Summary of the taphonomic processes leading to bone fossilization. (a) Preburial agents. (b) Postburial agents.

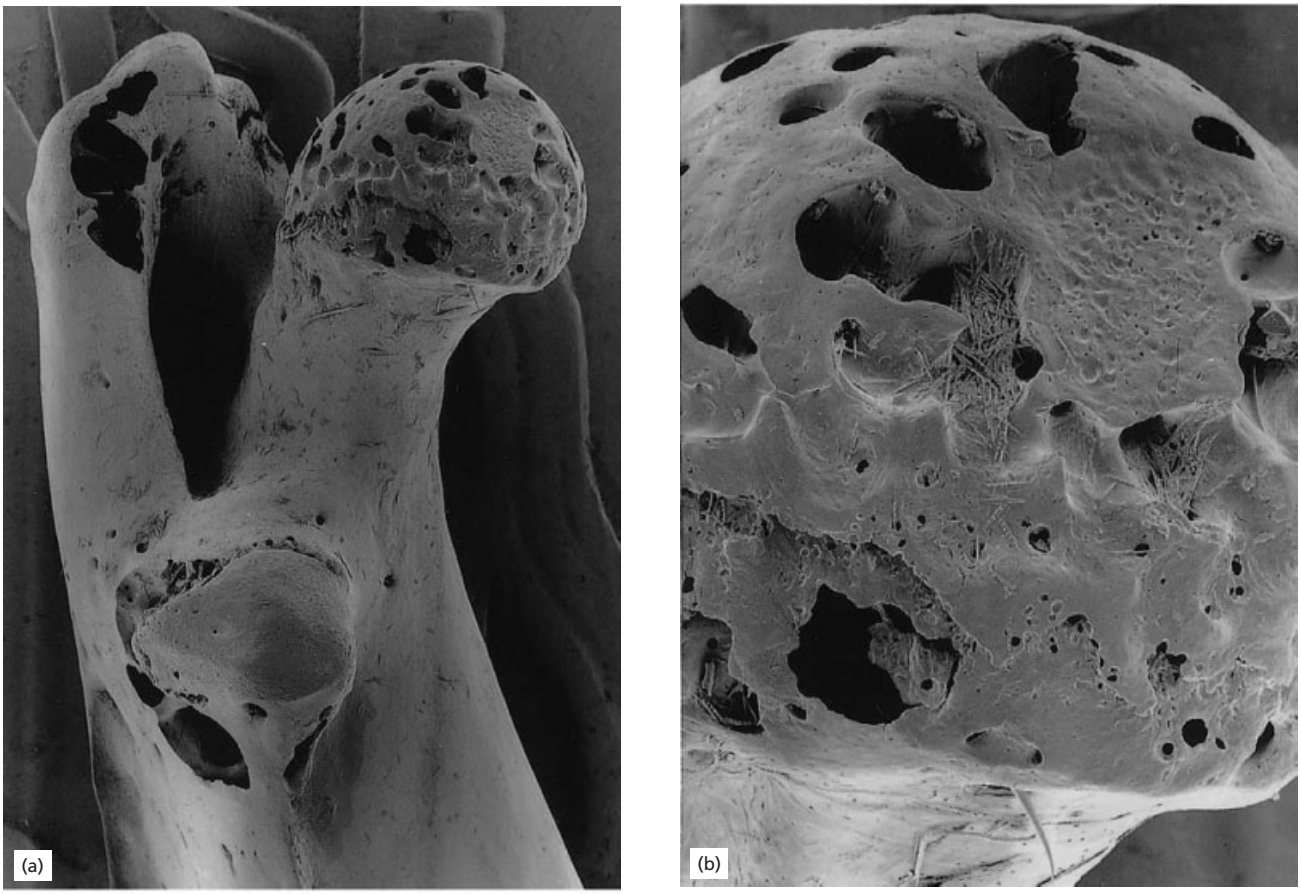

Fig. 3.1.8.2 (a) Moderate grade of digestion on a rat femur head produced by a captive spotted eagle owl, ×12.5. (b) Detail of the perforations and polished surfaces produced by digestion, ×41.

strontium, crystallographic alterations, and protein degradation.

Trampling also causes bone fragmentation, and can be recognized by parallel scratches on bone surfaces. Transport is the main process involved in the reworking of bones and the accumulation of mixed assemblages in fossil sites; abrasion by sediment typically causes rounding and polishing of bone surfaces (Fig. 3.1.8.5) (Andrews 1990). Water transport can result in the loss and dispersion of skeletal elements, or the sorting and concentration of bones, depending on density. The hydraulic equivalents of bones have been determined in terms of the diameter of a quartz sphere that would settle at the same velocity, thus defining five dispersal categories (Voorhies categories) from high (1) to low (5) (Table 3.1.8.3) (see Behrensmeyer 1975). This allows an assessment of the degree to which the hydraulic properties of bones are compatible with those of the surrounding sediment, and hence the likely source and homogeneity of the assemblage. The approach provides a tool to develop strategies for prospecting fossil sites. Bone density, rather than shape and size, is the main factor governing bone mobility; this explains why the Voorhies categories for homologous bones of both large and small mammals are nearly identical. Experiments have shown that mandibles and molars are the densest elements, and the least transportable. They require a high current velocity for entrainment, while the skull, vertebrae, and scapulae are less dense and more easily transported (Behrensmeyer 1975).

After burial (which can occur more than once, due to reworking), bones are subject to bioturbation (i.e. burrowing, dispersal by soil animals) and the effects of roots and lichens. Root growth can lead to dispersion and fragmentation; root markings on bone surfaces are common and take the form of characteristic sinuous traces (Fig. 3.1.8.6). Dissolution, recrystallization, and soil corrosion all affect the bone structure, whether by facilitating permineralization (and therefore preservation) or by promoting dissolution in acid or alkaline conditions. Diagenetic changes to bones have been documented at only a few Plio-Pleistocene sites in Africa

Table 3.1.8.1 Categories of incisor and molar digestion by avian predators (after Andrews 1990).

Digestion category	Molar digestion	Incisor digestion
1 Absent to very low digestion molars: 0–3% incisors: 8–13%	Short-eared owl Long-eared owl Barn owl Verreaux eagle owl	Short-eared owl Snowy owl Barn owl
2 Moderate digestion molars: 4–6% incisors: 20–30%	Spotted eagle owl Great grey owl Snowy owl	Verreaux eagle owl Great grey owl Long-eared owl
3 Strong digestion molars: 18–22% incisors: 50–70%	European eagle owl Tawny owl	European eagle owl Spotted eagle owl Tawny owl Little owl
4 Very strong digestion molars: 50–70% incisors: 60–80%	Little owl Kestrel Peregrine	Kestrel Peregrine
5 Extreme digestion molars: 50–100% incisors: 100%	Red kite Hen harrier Common buzzard	Hen harrier Common buzzard

Table 3.1.8.2 Predation categories (after Andrews 1990).

Category	Predators	Alterations
1	Barn owl Snowy owl Great grey owl	Few modifications Absent or light digestion
2	Long-eared owl Verreaux eagle owl Spotted eagle owl	Few modifications Light digestion—enamel absent from incisor tips
3	Tawny owl European eagle owl	More modification Moderate to strong digestion of enamel
4	Little owl Kestrel Peregrine Viverridae Mustelidae	Extreme digestion of dentine, enamel Extreme modification for mustelids but low percentage of digested elements
5	Common buzzard Red kite Canidae Felidae	Most destructive category Mammal carnivores produce rounded bone edges Teeth marks rare except for canids

(three lacustrine deposits, two karstic deposits) and in only one Oligocene karstic infill (Pech Crabit, Quercy, south-west France); while P content can be highly variable, an increase in Ca is usual (Fig. 3.1.8.3). The Ca/P ratio varies from 2.14 (Sterkfontein extension site, South Africa) to 2.36 (Olduvai Bed I, Tanzania); in modern bone it is 1.84. The enrichment of Ca, but also in other minor elements such as Mg, S, Fe, Sr, reflects the nature of the sediment and the depositional environment, rather than the duration of diagenesis.

Taphonomic context and history

Bone taphonomy has been analysed in different vertebrate assemblages and a methodology developed that can be applied to all types of vertebrates to determine the nature of bone modifications and their degree of diagenesis. Predation is the main agent of concentration for microvertebrate assemblages, and all predator categories are involved. Different sites in various contexts have been compared to provide a classification based either

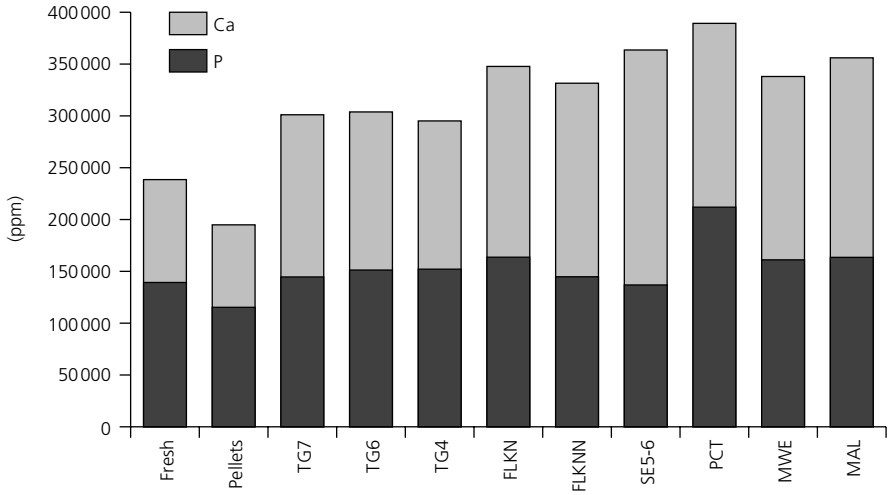

Fig. 3.1.8.3 Chemical composition changes of the major elements (P and Ca) of bone in fresh, digested (owl pellets), and fossil rodents. TG, Tighenif sites (Algeria), levels 4, 6, 7; FLK, Olduvai Bed I FLK sites (Tanzania), levels N and NN; SE5-6, Sterkfontein Extension site (South Africa); PCT, Pech Crabit site (France); MWE and MAL, Mwenerondo and Malema sites (Malawi) in Chiwondo Beds. (After Denys *et al.* 1997.)

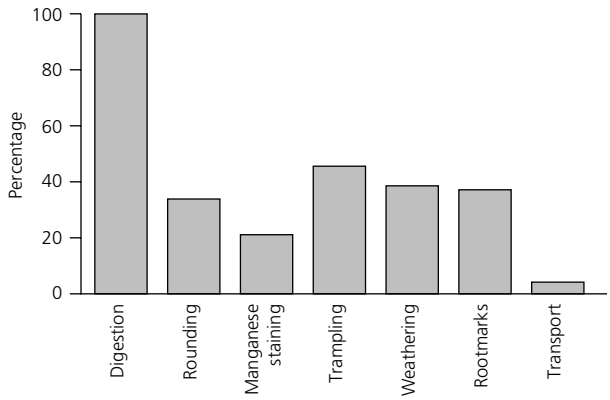

Fig. 3.1.8.4 Percentages of occurrences of the most frequent types of bone modifications at different Plio-Pleistocene sites studied by the taphonomic method of Andrews (1990). (After Denys *et al.* 1997.)

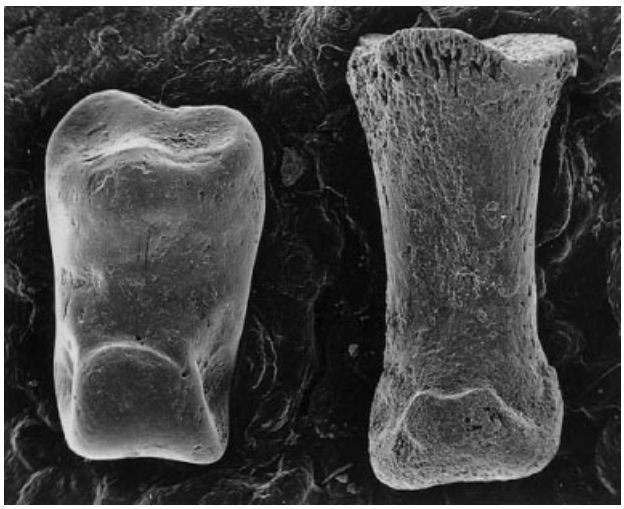

Fig. 3.1.8.5 Contrast between rounding and polishing after water transport (left) and soil corrosion (right) of the same skeletal element (*Cainotherium* phalanxes); Pech Crabit site (Oligocene, France), ×10.

on taphonomic alterations, depositional context, or sediment nature; such a classification attempts to provide a predictive tool for new sites (Denys *et al.* 1997). The degree of morphological and structural preservation of a bone is not correlated with its chemical composition nor with time. Similarly, changes in crystallinity, organic and mineral content, and surface and structural preservation are not time dependent, but are the result of taphonomic history and the context in which bones are deposited (Fernandez-Jalvo *et al.* 1998). Detailed taphonomic analysis provides information about the his-torical processes of bone preservation, site formation, and previous postburial environments; such an analysis is fundamental to enhancing qualitative and quantitative biostratigraphical, palaeoecological, and palaeobiogeographical interpretation.

Table 3.1.8.3 Bone behaviour or Voorhies categories (groups 1–5, from the most to the least easily removed bones) as a function of transport as determined experimentally (see Behrensmeyer 1975).

Bone/Taxa	Sheep/Dog	Sheep	Horse	Raccoon	Cottontail	Squirrel	Mouse	Deer mouse	Shrew
Atlas		2	2	2	2	2		2	2
Vertebrae	1						1 and 2	2	
Sacrum	1								
Sternum	1								
Ribs	1	1		1				1	
Skull	5	3	3	2	2	2	3	3	5
Pelvis	3				2		2	2	
Humerus	3						3	3	
Radius	3						4	2	
Ulna	2						4	2	
Scapula	2	3			3	3		1	
Femur	3		3	4	3	3	3	3	3
Tibia–fibula	3					5	3	5	
Astragalus			3	3	3	3		3	3
Calcaneum				3		3	4	3	3
Phalanges	2			3				1	
Metapodials	3							2	
Molars		3	3		3	3		4	4
Incisors								4	
Maxillae	5						1	3 and 4	
Mandible	4	4	5	5	5	5	5	4	5

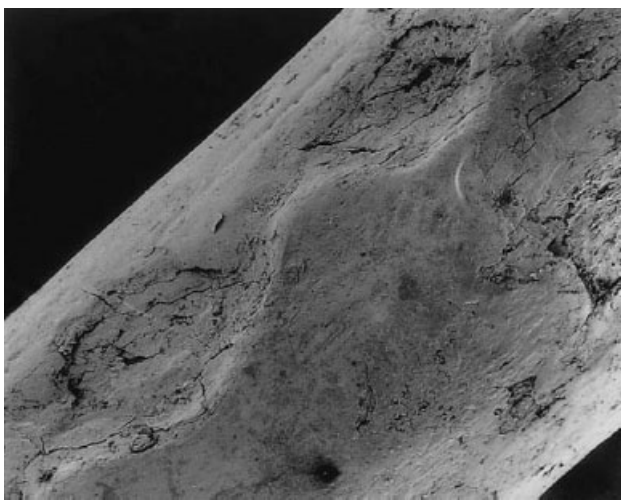

Fig. 3.1.8.6 Rootmarks on the surface of Holocene rat bone, ×20.

References

Andrews, P. (1990) *Owls, caves and fossils*. Natural History Museum Publications, London.

Behrensmeyer, A.K. (1975) The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolf, Kenya. *Bulletin of the Museum of Comparative Zoology of Harvard* **146**, 473–578.

Dauphin, T., Denys, C. and Kowalski, K. (1997) Analysis of rodent remains accumulations: role of the chemical composition of skeletal elements. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **203**, 295–315.

Denys, C., Andrews, P., Dauphin, Y., Williams, T. and Fernandez-Jalvo, Y. (1997) Towards a site classification: comparison of stratigraphic, taphonomic and diagenetic patterns and processes. *Bulletin de la Société Géologique de France* **168**, 751–757.

Fernandez-Jalvo, Y., Denys, C., Andrews, P., Dauphin, Y. and Humphrey, L. (1998) Taphonomy and palaeoecology of Olduvai Bed-I (Pleistocene, Tanzania). *Journal of Human Evolution* **34**, 137–172.

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3.2 Fossilization Processes

3.2.1 Decay

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Introduction

Naturally occurring, biologically synthesized molecules are a valuable food resource and the heterotrophic part of the Earth's ecosystem is dependent upon them. It is no surprise therefore that organic matter is utilized by microbes as a food resource. The decay of organic matter is the *bête noire* of the palaeontologist. Up to two-thirds of the diversity and abundance of metazoans in modern shallow-water environments are entirely soft-bodied. Upon death, such organisms are usually destroyed by microbes before they can be fossilized. The preservational bias imparted by decay is not restricted to soft-bodied organisms but also affects those with multielement mineralized skeletons that are held together by soft tissues. The decay of connective tissues allows differential transport of skeletal elements and promotes disarticulation. This is particularly common for vertebrate remains and many invertebrate fossils, such as crinoids and trilobites; decay is typically rapid and even the gentlest of currents is capable of transporting their disarticulated elements. The preservation of articulated multielement skeletons is therefore an indicator of rapid burial.

Decay

Decomposition is usually rapid and is only delayed in geologically short-term circumstances, such as extreme aridity and very low temperatures. Carcasses preserved by desiccation or deep freezing will begin to decay following climatic change and rehydration or thawing. However, carbonized soft parts are found as fossils. Plants are commonly found preserved in this way but animal remains can also be carbonized. Well-known examples include the Middle Cambrian Burgess Shale and deposits of similar age (Allison and Briggs 1991) but more geologically abundant examples include many graptolite-bearing shales where periderm has been preserved. Although such preservation is structurally impressive, with cortical bundles preserved in graptolites and cuticular ultrastucture preserved in *Wiwaxia*, for example (Butterfield 1990), the chemistry of the primary tissue does not survive. The original molecule is diagenetically transformed. However, this is not the case with all preserved organic tissues. For example, chitin (the structural polysaccharide in arthropod cuticle) has been recovered from insect cuticle in Oligocene lake sediments (Stankiewicz *et al.* 1997) (see Section 3.1.6). Thus there are environments where preservation can include molecular detail. An understanding of preservation must be based upon a knowledge of decay and the ecology of the organisms responsible for it. The rate of decay is influenced primarily by environmental conditions and the nature of organic carbon.

In the presence of oxygen, decay is usually rapid. The principal by-products of this reaction are water and carbon dioxide. Once oxygen has been depleted, decay does not cease but proceeds through a series of alternative reactions broadly termed *anaerobic*. The sequence in which these oxidants are utilized is governed by their free-energy yield during respiration. In ideal circumstances they are stratified in the sediment profile (Fig. 3.2.1.1), those liberating the highest free-energy yield occurring highest in the sequence (Berner 1981). Reactions lower in the sediment profile only operate following the complete reduction of ions required for the more efficient ones. However, the supply of these oxidants is not uniform. Nitrate reduction and methanogenesis dominate in a freshwater environment, whereas sulphate reduction and methanogenesis dominate in marine regimes. The depth to which these reactions are active in the sediment depends upon organic supply, temperature, and sediment permeability. A greater input of organic detritus increases demand for the ions required for anaerobic respiration. Reduced permeability impedes the transfer of these ions from the overlying water column to porewaters, and temperature increases the rate of decay. Increased demand and reduced supply leads to the attenuation of the layered reduction zones. In the most extreme case, the anoxic–oxic boundary lies above the sediment–water interface.

Prolonged exposure to oxygen can lead to the complete destruction of organic carbon in sediment by aerobic bacteria. However, anaerobic bacteria are less efficient biodegraders and may be unable to break down complex biopolymers completely. Bacterial utilization of refractory organic carbon in sediment may require the presence of a bacterial community composed of a range of reducing bacteria (e.g. aerobic bacteria, nitrate-reducers, manganese-reducers, etc.) (Jørgensen 1983). In

AEROBIC DECAY

$$(CH_2O)_{106}(NH_3)_{16}H_3PO_4 + 106\,O_2 \longrightarrow 106\,CO_2 + 16\,NH_3 + H_3PO_4 + 106\,H_2O$$

ANAEROBIC DECAY

Manganese reduction

$$(CH_2O)_{106}(NH_3)_{16}H_3PO_4 + 212\,MnO_2 + 332\,CO_2 + 120\,H_2O \longrightarrow 438\,HCO_3^- + 16\,NH_4^+ + HPO_4^{2-} + 212\,Mn_4^{2+}$$

Nitrate reduction

$$(CH_2O)_{106}(NH_3)_{16}H_3PO_4 + 84.8\,NO_3^- \longrightarrow 7.2\,CO_2 + 98.8\,HCO_3^- + 16\,NH_4^+ + 42.4\,N_2 + HPO_4^{2-} + 49\,H_2O$$

Iron reduction

$$(CH_2O)_{106}(NH_3)_{16}H_3PO_4 + 424\,Fe(OH)_3 + 756\,CO_2 \longrightarrow 862\,HCO_3^- + 16\,NH_4^+ + HPO_4^{2-} + 424\,Fe^{2+} + 304\,H_2O$$

Sulphate reduction

$$(CH_2O)_{106}(NH_3)_{16}H_3PO_4 + 53\,SO_4^{2-} \longrightarrow 39\,CO_2 + 67\,HCO_3^- + 16\,NH_4^+ + HPO_4^{2-} + 53\,HS^- + 39H_2O$$

Methanogenesis (carbonate reduction)

$$(CH_2O)_{106}(NH_3)_{16}H_3PO_4 + 14\,H_2O \longrightarrow 39\,CO_2 + 14\,HCO_3^- + 53\,CH_4 + 16\,NH_4^+ + HPO_4^{2-}$$

Fermentation

$$12(CH_2O)_{106}(NH_3)_{16}H_3PO_4 \longrightarrow 106\,CH_3CH_2COOH + 106\,CH_3COOH + 212\,CH_3CH_2OH + 318\,CO_2 + 102\,H_2 + 192\,NH_3 + 12\,H_3PO_4$$

Fig. 3.2.1.1 Idealized decay profile of disseminated organic carbon (with the composition of marine plankton) in aquatic sediment. Under anaerobic conditions, nitrate reduction, iron reduction, and methanogenesis dominate in freshwater settings, while sulphate reduction and methanogenesis dominate in marine environments. (Adapted from Berner 1981 and Allison and Briggs 1991.)

such an environment, each group of bacteria partially degrades the more complex molecules to produce by-products which other bacteria (lower down the chemically stratified column) use in the respiration process. In this model, preservation of complex biopolymers would be favoured in euxinic settings where the bacterial reduction zones are severely attenuated and the microbial food chain is broken. However, the geochemical understanding of decay is based primarily upon considerations of disseminated organic carbon. Organisms are concentrations of organic carbon. The demand for oxygen during aerobic decay is very high. One mole of organic carbon (Fig. 3.2.1.1) weighs 3.533 kg and requires 106 moles of oxygen that occupy 2374 l. Thus 1 g dry weight of organic matter requires 672 cm^3 of oxygen for complete decay. Put another way, a medium-sized fish weighing 1 kg contains ≈70 g dry weight of organic carbon compounds and requires about 47 l of oxygen for complete decay. If sea water contains ≈5 ml/l of dissolved oxygen, then the fish is capable of depleting the oxygen from 9400 l of oxygenated sea water, i.e. a body of water weighing nearly 10 tonnes and occupying a volume of 9.4 m^3. Since the outer surface of most organisms is covered by a skin that prevents oxygen diffusing in, and given the vast demand for oxygen during aerobic decay, it is not surprising that most carcasses decompose anaerobically.

The same principles apply to the supply of the other oxidized compounds that are used during anaerobic decay. The decay of a fish on the sediment surface would very quickly change from aerobic to anaerobic. Manganese reduction is unlikely to be involved, however, because manganese oxide is insoluble and cannot pass through the skin of the fish to fuel the process. Iron reduction can occur through the reduction of iron-bearing compounds in haemoglobin-based blood. Thus the decaying flesh of vertebrate carcasses often assumes a green tint due to the reduction of iron in the blood. Decay of large carcasses by sulphate reduction is impeded in much the same way as aerobic decay, simply because sufficient sulphate cannot migrate into the carcass to fuel sulphate-reducing bacteria. As a result, most large carcasses decay through fermentation and methanogenesis. For example, the flesh around wounds affected by gas gangrene (generated by *Clostridium*) decomposes by rapid methanogenesis despite the patient being in air, with an oxygen concentration close to 20%.

Organic biomolecules are composed primarily of carbon, oxygen, nitrogen, phosphorus, and sulphur arranged in a variety of structural forms. Rates of decay are heavily influenced by the proportion and arrangement of these elements. For example, polymers composed of repetitions of the same monomer, or with a limited variety of bond types, are broken down more quickly than those with a variable monomer composition or bond diversity. In addition, certain bond types, such as carbon–carbon bonds, may impart decay resistance. Although the pattern of molecular diversification through time is unknown, it is likely that the diversity and complexity of carbon molecules on Earth today is greater than it was in the Precambrian. One of the most significant events in molecular diversification was the evolution of the aromatic compound lignin in plants. Terrestrialization in the Late Devonian and Carboniferous established a biosphere on land which acted as a

reservoir for organic carbon drawn down from the atmosphere. Plants flourished in low-lying basins prone to flooding. After death, much of the plant material was deposited in these waterlogged bogs where partial decay generated organic acids and halted the decay of structurally complex molecules such as lignin. The atmospheric carbon incorporated into the biosphere could not be recycled by bacteria and became fossilized as coal and stored in the lithosphere. This caused a significant reduction in levels of atmospheric CO_2 (Fig. 3.2.1.2). The efficiency of the biodegrader community has a powerful effect on global biogeochemical cycles. It has been estimated that the fortuitous combination of biological innovation (evolution of lignin use) and environmental setting (low-lying paralic basins) caused atmospheric CO_2 to fall from 10 times today's levels in the Devonian to almost modern values by the end of the Carboniferous (Van Andel 1994).

Decay inhibition

The decay of a concentration of organic tissue like a carcass can be impeded by a process that does not affect disseminated organic matter to the same extent. The rate at which microbes function is limited by the supply of nutrients and the rate at which their metabolic by-products are removed. Few organisms can function successfully bathed in their own metabolic by-products. Given that large carcasses decay by fermentation, the body will eventually fill with metabolic by-products that may reduce the activity of the decomposing community. A variety of echinoderms sealed in containers of sea water with an inoculation of microbe-bearing anoxic mud decayed slowly; specimens sampled after 6 months were remarkably intact (Allison 1991). Asteroids and echinoids were still articulated and some holothurians remained recognizable. It seems likely that the decay rate achieved by the microbes was reduced by the toxicity of their metabolic by-products that built up in the closed system. This condition could easily be magnified in a natural setting if the carcass were covered by a microbial mat. The mat would inhibit both the infusion of oxygen and sulphate and the diffusion away of toxic metabolites. The experiments also showed that different organisms of apparently similar architecture decayed at markedly different rates (varying by a factor of two or three). This was most likely due to biochemical variations in the composition of the different organisms. The bias imposed by decay is pervasive, even in circumstances where some soft parts are preserved.

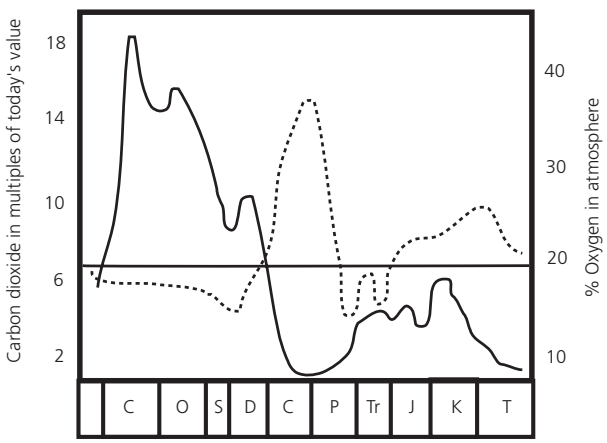

Fig. 3.2.1.2 Interpreted changes in atmospheric levels of O_2 (dashed line) and CO_2 (solid line) through the Phanerozoic. The horizontal line represents the current level of O_2. (Replotted from Van Andel 1994.)

Clay minerals may also retard the decay process. Microbes digest carbon compounds by using extracellular enzymes. This produces soluble biomolecules that are absorbed back through the cell membrane. In natural sedimentary systems, however, the organic carbon (whether in the form of carcasses or disseminated fragments) is mixed with sedimentary grains. Under certain conditions microbial digestive enzymes are adsorbed on to the mineral surfaces, and thus rendered inoperative (Butterfield 1990). Well-preserved organic fossils are almost exclusively limited to fine-grained mudrocks. The clay minerals that make up mudrocks are small and platy, with a relatively large surface area and the potential to adsorb a considerable volume of enzymes. Although this is an appealing hypothesis that has been experimentally proven as a mechanism to reduce decay rate of disseminated carbon in soils (see Butterfield 1990), it has not yet been experimentally proven (or disproven) as a mechanism to preserve metazoans in marine sediments. Clay minerals may also influence decay rate by plating on to organic remains during deposition. This would serve to inhibit the supply of compounds for microbial reduction and would also prevent the diffusion away from the carcass of toxic metabolites. Clay mineral plating has been invoked as a mechanism to explain preservation in the Middle Cambrian Burgess Shale (Butterfield 1990).

Decay can be halted by reactions between porewater ions and organic by-products. The decay of fats and proteins liberates fatty acids in a locally alkaline setting. These can react with ions such as calcium to produce natural soaps (see Allison and Briggs 1991). It was once thought that soaps represented an intermediary stage in carbonate formation, but this is now recognized not to be the case. However, short-term (tens or hundreds of years) preservation of soft tissues as soaps has been documented many times. Although the soaps themselves may not survive for geologically significant periods of time, the process of soap formation may still be important as it increases the residence time of soft

tissues in sediment. The longer that soft tissues survive, the greater the chance that diagenesis may occur and preserve the tissues over a longer term.

Destruction of soft-tissue morphology can also be reduced by mineralization. Anaerobic degradation reactions (Fig. 3.2.1.1) generate a series of chemically reactive compounds that include HCO_3^-, HPO_4^{2-}, and H_2S. These compounds react with metal ions to produce minerals. Such diagenetic reactions can be rapid and can preserve tissues. Early experiments (Allison 1988) showed that, although decay-induced information loss was rapid, precursors to pyrite formed within weeks or months. Later experiments (Hof and Briggs 1997) have shown that carbonate and phosphate minerals can preserve cellular detail within weeks. The rate at which minerals form varies in different species. Calcium phosphate mineralization was more rapid in mantis shrimps than it was in decapod crustaceans, reflecting the chemical composition of the cuticle of the two species. Thus, not only does decay rate differ between different soft-bodied organisms (Allison 1991) but the mineralization generated by the decay can also vary (Hof and Briggs 1997). More importantly, rate of decay is influenced by the influx of nutrients and the outward diffusion of metabolites, dependent upon the porosity and permeability of the entombing sediment. This can fluctuate within a factor of two or three in intertidal beach sands (see Allison 1991).

References

Allison, P.A. (1988) The decay and mineralization of proteinaceous macrofossils. *Paleobiology* **14**, 139–154.

Allison, P.A. (1991) Variation in rate of decay and disarticulation of Echinodermata: implications for application of taphonomic data. *Palaois* **5**, 432–440.

Allison, P.A. and Briggs, D.E.G. (1991) Preservation of soft-tissues. In: P.A. Allison and D.E.G. Briggs, eds. *Taphonomy: releasing the data locked in the fossil record*, pp. 25–70. Plenum Press, New York.

Berner, R.A. (1981) Authigenic mineral formation resulting from organic matter decomposition in modern sediments. *Fortschritte der Mineralogie* **59**, 117–135.

Butterfield, N.J. (1990) Organic preservation of non-mineralizing organisms and the taphonomy of the Burgess Shale. *Paleobiology* **16**, 272–286.

Hof, C.H.J. and Briggs, D.E.G. (1997) Decay and mineralization of mantis shrimps (Stomatopoda: Crustacea)—a key to their fossil record. *Palaois* **12**, 420–438.

Jørgensen, B.B. (1983) Processes at the sediment–water interface. In: B. Bolin and R.B. Cook, eds. *The major biochemical cycles and their interactions*, pp. 477–561. J. Wiley and Sons, Chichester.

Stankiewicz, B.A., Briggs, D.E.G., Evershed, R.P., Flannery, M.B. and Wuttke, M. (1997) Preservation of chitin in 25-million-year-old fossils. *Science* **276**, 1541–1543.

Van Andel, T.H. (1994) *New views on an old planet*. Cambridge University Press, Cambridge.

3.2.2 Bioerosion

E.N. EDINGER

Introduction

Bioerosion is an important taphonomic agent in most marine environments, and can be divided into internal and external bioerosion. The principal controls on bioerosion are productivity, sedimentation, substrate durability, and water depth. Bioerosion typically leaves trace fossils that can have important applications in palaeoecology (Bromley 1994). The intensity and type of bioerosion evident in fossils can yield information about rate of burial, depositional environments, palaeoproductivity, and preservation style, particularly in coral reefs (see Section 3.3.3). Increased intensity of bioerosion through geological time follows the origination of new groups of bioeroding organisms, with additional influence from variations in marine productivity.

Marine bioeroding organisms

There are three major types of marine bioeroding organisms: microborers, internal macroborers, and external raspers or scrapers (Table 3.2.2.1). Microborers are primarily filamentous endolithic algae and fungi. Macroborers do not eat their host substrates, but excavate dwellings within them, where they are protected from predation. The relative importance of microboring, macroboring, and grazing varies with depth, sedimentation rate, and productivity.

Macroborers

Boring sponges excavate their substrates by a combined chemical–mechanical process, typically dissolving less than 5% of the material that they remove. The remaining material is eliminated as distinctive silt-sized chips of debris, leaving the inner sides of sponge borings with a characteristic scalloped texture.

The four major groups of boring bivalves vary in their distribution and modes of excavation (Kleemann 1996). In tropical waters, lithophagid and gastrochaenid bivalves biocorrode chemically into carbonate rocks, corals, mollusc shells, and similar materials. Pholad bivalves, with strongly ridged shells, bore mechanically into a variety of rock types, primarily in temperate regions. Wood-boring bivalves are common in floating and sunken wood in a wide variety of marine, brackish, and some freshwater environments. Shipworms have extraordinarily long calcite-lined siphonal canals, and

Table 3.2.2.1 Major groups of bioeroding organisms, with their trace fossil names, description of boring or scraping morphology, age range, and depth range. Also included are macroborer look-alikes, i.e. organisms which inhabit corals and deform coral growth around them, but do not actually bioerode skeletal material.

Organisms	Trace fossils	Description	Age range	Depth range
Microborers				
Filamentous green algae	Many names	Filaments, 10–50 µm diameter	Precambrian–Recent	Photic zone
Cyanobacteria		Filaments, 2–10 µm diameter	Precambrian–Recent	Photic zone
Fungi		Filaments, < 2 µm diameter	Precambrian–Recent	All depths
Macroborers				
Sponges	*Entobia*	Multiple small chambers, connecting filaments	Ordovician–Recent	All depths
	Uniglobites	Large rounded chambers, broad papillae	Triassic–Recent	Primarily shallow
Bivalves	*Petroxestes*	Facultative borer	Ordovician–Silurian	Shallow
Lithophaga, *Gastrochaena*, Pholadidae	*Gastrochaenolites*	Clavate borings in rock, coral, shell, may be lined	Carboniferous–Recent	Primarily shallow
Teredo, Xylophaginae	*Teredolites*	Elongate carbonate-lined tubes in wood	Cretaceous–Recent	Primarily shallow
Worms (in general)	*Trypanites*, *Lapispecus*	Straight cylindrical holes	Cambrian–Recent	Primarily shallow
Polydorids	*Caulostrepis*	Small U-shaped tubes	Ordovician–Recent	All depths
	Maeandropolydora	Large anastomosing tubes	Ordovician–Recent	All depths
Phoronids	*Talpina*	Small branched tubes	Ordovician–Recent	All depths
Ctenostome bryozoans	*Ropalonaria*, *Voigtella*, *Spathipora*, *Foraripora*, *Penetrantia*	Small elongate regular chambers, usually in branched networks	Ordovician–Recent	All depths
Cheilostome bryozoans	*Leptichnus*	Shallow surface etchings, small ovate units arranged in fan-shaped or branching clusters	Cretaceous–Recent	Primarily shallow
Brachiopods	*Podichnus*	Pedicle attachment scars	Ordovician–Recent	Mostly deep
Acrothoracican barnacles	*Rogerella*, *Zapfella*, others	Large, pocket-shaped, with slit-shaped apertures	Silurian–Recent	Primarily at surface
Upogebia	Similar to *Spongeliomorpha*	Broad U-shaped galleries with 2–3 narrow apertures	Jurassic–Recent	Primarily at surface
Beetles and other insects	*Stipitichnus*	Elongate, anastomosing tubes with larval galleries	Carboniferous–Recent	Terrestrial
Macroborer look-alikes				
Lithophaga (Leiosolenus)	n/a	Deform coral growth, but do not bioerode	Pliocene–Recent	Shallow
Pyrgomatine barnacles	n/a	Deform coral growth, but do not bioerode	Miocene–Recent	Shallow
Grazers				
Limpets and chitons	*Radulichnus*	Small parallel scrape marks on rocks	Cambrian–Recent	Primarily at surface
Regular echinoids	*Gnathichnus*	Larger pentamerous scrape marks	Jurassic–Recent	Photic zone
Acanthurid and scarid fish	No name	Gouges, deep scrape marks	Miocene–Recent	Photic zone

are an economically and historically important threat to wooden ships—the Spanish Armada that sailed against England in 1588 was sunk primarily by shipworms.

Polychaete and sipunculan worms excavate borings in corals, shells, hardgrounds, other carbonates, and in some fine-grained clastic sedimentary rocks. Polydorid worms are usually among the first macroborers to colonize carbonate materials. Ctenostome bryozoans chemically excavate borings that resemble small multichamber sponge borings, but the size, shape, and spacing of the

chambers are smaller and more regular than those produced by sponges. Ctenostomes were common in Palaeozoic brachiopod shells, but are now relatively rare in most shallow marine substrates. Some brachiopods etch pedicle borings, known as *Podichnus*, where they attach to hard substrates. Gall crabs, the thalassinid shrimp *Upogebia*, and acrothoracican barnacles are the major groups of boring crustaceans. Acrothoracican barnacle borings were common in floating substrates like belemnite rostra, and modern acrothoracicans are most abundant at sea level.

External grazers and raspers

External bioeroders feed on algae in the surface layers of corals and sedimentary rocks, and their activities are necessarily limited to the photic zone. Chitons and limpets bioerode as they graze epilithic algae on rocky coastlines. Echinoids and parrotfish grazing on endolithic algae in corals consume large amounts of coral skeleton, and defecate carbonate sand.

Predation can sometimes involve bioerosion. Some predatory molluscs bioerode the shells of their prey. Gastropods drill through the shells of their molluscan prey, creating bevelled (naticid) or straight (muricid) holes through the shells, known as *Oichnus*. Octopus predation can make similar trace fossils. Shell- or bone-crushing predation and other forms of durophagy are discussed in Sections 3.3.7 and 4.1.7. Terrestrial bioerosion (Mikulas 1999) is not covered here.

Controls on rate and intensity of bioerosion

Bioerosion rates can be measured experimentally in modern substrates in a variety of environments, while bioerosion intensity refers to the amount of material removed over time, and can be measured using survey-based approaches in both modern and fossil material. Four major factors control rates of bioerosion: biological productivity, rate of burial, water depth, and the density and architecture of the substrate (Fig. 3.2.2.1). Most macroborers are heterotrophic filter feeders: they grow faster, and consequently bioerode more material, in more productive waters. Similarly, growth of the endolithic algal microborers upon which external bioeroders graze is stimulated by nutrients. Thus all types of bioerosion increase with marine primary productivity.

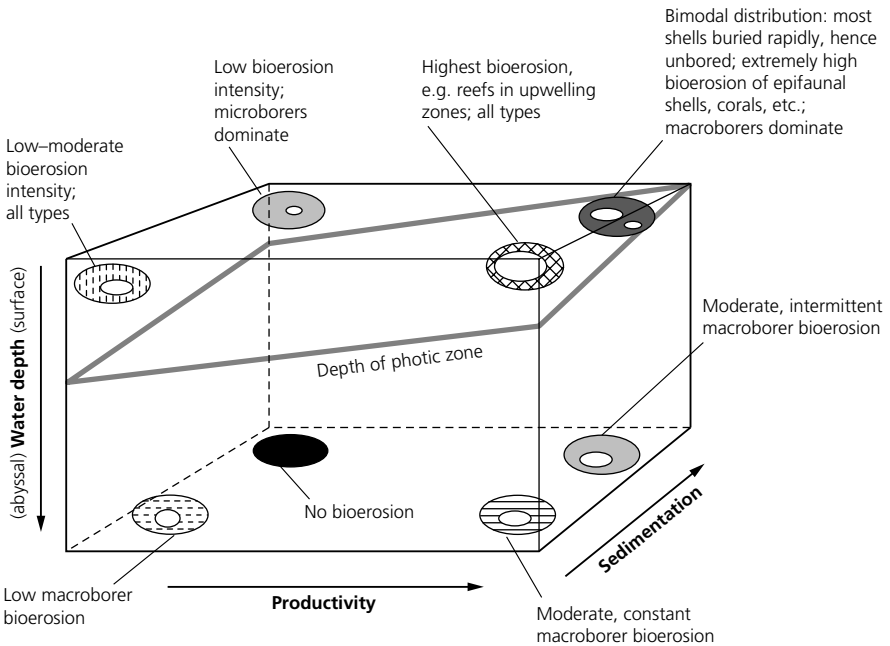
Bimodal distribution: most shells buried rapidly, hence unbored; extremely high bioerosion of epifaunal shells, corals, etc.; macroborers dominate
Low bioerosion intensity; microborers dominate
Highest bioerosion, e.g. reefs in upwelling zones; all types
Low–moderate bioerosion intensity; all types
(abyssal) Water depth (surface)
Depth of photic zone
Moderate, intermittent macroborer bioerosion
No bioerosion
Sedimentation
Low macroborer bioerosion
Productivity
Moderate, constant macroborer bioerosion

Fig. 3.2.2.1 The major controls on bioerosion intensity are depth, productivity, and sedimentation. Bioerosion rates increase with productivity and decrease with sedimentation and depth. The highest internal and external bioerosion rates are found in shallow, high productivity, low sedimentation environments, such as coral reefs in upwelling zones. Under shallow, high productivity, high sedimentation conditions, shells have a bimodal distribution of bioerosion, in which most shells are rapidly buried and unbored, but the remaining shells are highly bioeroded. Below the photic zone, bioerosion is limited to macroborers and fungi, and rates of bioerosion are several orders of magnitude lower than in the photic zone. The depth limit of the photic zone shallows with increasing productivity and sedimentation, both of which increase turbidity. In most deep-sea environments, the residence time of shells at the surface is long, yielding moderate to high bioerosion intensities. Deep-sea bioerosion is dominated by boring sponges, worms, and bryozoans.

Residence time of material at the sediment–water interface influences bioerosion intensity. Rapid burial isolates material from bioeroding organisms and prevents bioerosion, while reworking of sediment can expose shells to repeated attack by bioeroding organisms. When both productivity and sedimentation rates are high, shells exhibit a bimodal distribution of bioerosion; most shells are rapidly buried and minimally bored, but those shells that are not buried have high bioerosion intensities.

Boring apertures on the inside of mollusc shells indicate postmortem boring (see Section 4.3.1); the ratio of boring apertures on insides to outsides of shells increases with postmortem residence time. A dearth of bioerosion on fossils indicates rapid sedimentation and burial, particularly if encrusting organisms are also rare (see Section 4.2.8).

Bioerosion rates decrease by several orders of magnitude below the photic zone, due to the absence of algal microboring and external grazing upon endolithic algae. Detrital organic matter is also less abundant in deep water, so macroborers grow more slowly. None the less, fossils in deep-water environments are frequently exposed to bioeroding organisms for a long time because sedimentation rates are generally low. Hence the intensity of bioerosion of deep-sea corals and shells can be moderate to high, resulting in the removal of 10–70% of the original skeleton.

Harder or more dense substrates are bioeroded at slower rates than softer or less dense materials. Many borers follow planes of weakness within the substrates they bore, such that boring morphology is partly determined by host skeletal architecture. Mollusc shells with high organic matrix content are bioeroded more rapidly than those with less organic matrix.

Bioerosion rates and succession in bioeroding organisms

Microborers are usually the first bioeroding organisms to colonize fresh substrates, and can cover 50% of fresh carbonate material in 2 months. As soon as endolithic algae accumulate significant biomass, grazers initiate external bioerosion, typically within 6 months; grazing bioerosion accounts for 70–90% of total bioerosion on many coral reefs (Glynn 1997). Grazing activity restricts internal macroborer bioerosion by removing larvae and juveniles of boring sponges and bivalves.

Macroborer bioerosion increases in importance with the exposure time of the substrate. The first macroborers are usually polychaete worms, which colonize fresh substrate within 2–6 months. Boring sponges and bivalves typically require 2–3 years to colonize substrates and grow large enough to cause significant bioerosion; boring sponges are usually the dominant macroborer of corals, especially in deep-water environments.

Succession and tiering in bioeroding communities results from the relative colonization times and boring depths of different types of borers. Early successional grazing and shallow microboring trace fossils comprise the *Gnathichnus* ichnofacies, while later arriving, slower acting, deeper macroborings, which frequently obliterate the *Gnathichnus* ichnofacies, comprise the *Entobia* ichnofacies.

Rates of bioerosion accelerate with succession of the bioeroding fauna. Microborers infecting coarse carbonate sand grains on coral reefs cause 3% weight loss per year, while macroborers and external grazers can each increase this rate by up to five times (Chazottes *et al.* 1995). In nutrient-rich coastal environments, bioerosion rates may be up to an order of magnitude higher, and at times may exceed total carbonate production (Glynn 1997).

Shells in shallow water can escape microboring only by rapid burial. The half-life of shells in different environments varies depending on shell structure, burial and exhumation rates, bioerosion rates, and shell breakage. Exposed shells in shallow nutrient-rich environments may have half-lives of less than 5 years, and shells that are not buried shortly after death are unlikely to be preserved.

Measuring bioerosion in fossils

Measurements of borehole size and/or frequency counts of sponge, bivalve, and other borings can be used to estimate bioerosion intensity. Borehole size measurements of single chamber sponge borings are roughly indicative of bioerosion intensity, as are counts of the number of chambers in multichamber sponge borings. Frequency counts of bivalve apertures in whole corals can be problematic because apertures of true borings are difficult to distinguish from dwellings of bivalves that displace coral skeletal growth (Table 3.2.2.1), but do not actually bioerode the coral skeleton. Frequency counts of all bioeroding organisms in coral rubble estimate bioerosion well, but require large volumes of material. Frequency counts of all boring types in a large number of fossil shells can estimate intensity and pattern of palaeobioerosion.

Bioerosion studies in palaeoecology

Palaeobathymetry (see Section 4.3.4) can be inferred from the distribution of microborings and external grazing bioerosion, while macroboring distribution is a better indicator of salinity, sedimentation rate, and oxygenation. Endolithic algae and grazing traces indicate deposition in the photic zone. Presence of fungal borings

without algal borings indicates exposure below the photic zone. Acrothoracican barnacle borings in limestones can be used as sea-level markers. Presence of *Podichnus* on shells in grey or black shales, in the absence of other macroborings, may indicate brachiopod colonization and growth under dysaerobic conditions.

Palaeoproductivity can be inferred from variation in bioerosion intensity, if other major controls are taken into account. The intensity of bioerosion in similar hosts in similar facies of different ages can be used to infer changes in marine productivity through time. Rapid encrustation by algae or animals restricts bioerosion. High frequency of encrustation, combined with high frequency of boring, indicates high productivity, low sedimentation conditions.

Geological history of bioerosion

The geological history of bioerosion is defined largely by the origins of major bioeroding taxa (Vogel 1993). The earliest recorded macroborings are *Trypanites* in Lower Cambrian archaeocyathid reefs. Sponge and bryozoan borings are known in Ordovician and younger rocks. The Ordovician facultative boring bivalve, *Corallidomus*, made *Petroxestes*, while the earliest known obligate boring bivalves (the producers of *Gastrochaenolites*) are Carboniferous. Most other groups of macroborers and external grazing invertebrates either arose or greatly expanded their diversity during the Mesozoic marine revolution (see Section 1.4.1). The major expansion of the *Teredolites* ichnofacies occurred in the Cretaceous. The earliest recorded coral-grazing fish are Miocene. Other major controls on bioerosion through time are related to variation in marine productivity.

References

Bromley, R.G. (1994) The palaeoecology of bioerosion. In: S.K. Donovan, ed. *The palaeobiology of trace fossils*, pp. 134–154. John Wiley, New York.

Chazottes, V., Le Campion-Alsumard, T. and Peyrot-Clausade, M. (1995) Bioerosion rates on coral reefs: interactions between macroborers, microborers, and grazers (Moorea, French Polynesia). *Palaeogeography, Palaeoclimatology, Palaeoecology* **113**, 189–198.

Glynn, P.W. (1997) Bioerosion and coral-reef growth: a dynamic balance. In: C.E. Birkeland, ed. *Life and death of coral reefs*, pp. 68–95. Chapman and Hall, New York.

Kleemann, K. (1996) Biocorrosion by bivalves. *Marine Ecology* **17**, 145–158.

Mikulas, R. (1999) Subaerial animal and plant bioerosion in castellated sandstone rocks (Pleistocene–Recent, Czech Republic). *Bulletin of the Geological Society of Denmark* **45**, 177–178.

Vogel, K. (1993) Bioeroders in fossil reefs. *Facies* **28**, 109–114.

3.2.3 Preservation by Fire

A.C. SCOTT

Introduction

Wildfire plays an important role in many of today's ecosystems (Crutzen and Goldammer 1993) and has played an important role on Earth for over 325 million years (Scott 2000). The extinguishing of fire may lead to a build-up of fuel with the consequence that an even more intense fire may result in the future. Most fires are started by lightning strikes—8 million occur every day. Eight billion tonnes of vegetation are burned each year by natural wildfires, which happen not only in temperate forests but also in the tropics and even in peat-forming wetlands. Not only vegetation is affected; some animals may be killed, but others may benefit from new plant growth.

There are three main types of fire: (1) crown fires where the areal parts of living trees are burnt; (2) surface fires which burn shrubs, herbs, and dead plant litter; and (3) ground fires which burn the organic layers in a soil or peat. Such fires are often seen as purely destructive but in fact they serve to promote fossilization (Scott 1989). Plant material may be totally consumed by the hot flames which are fed with oxygen from the air; but air may be excluded from the centre of large trunks or branches or from the plant litter. Charring occurs, therefore, when there is heat and a lack of oxygen. Large quantities of charcoal may result from incomplete combustion of living vegetation and also of the plant litter layer. In addition to charring by wildfire, vegetation may be charred by contact with hot lava or ash. Moisture and volatile components (e.g. gases such as CO_2, CH_4, and liquids) are driven off and the cell walls are converted to almost pure carbon. The temperature reached during the charring process has an effect upon the physical and chemical characteristics of the resulting charcoal. In the oxygen-fed flames of an intense crown fire, the temperature may exceed 1000°C and plant material may be completely combusted; yet in the surface plant litter the temperature may only reach a few hundred degrees (Rundel 1981), resulting in the charcoalification of plant tissues.

Charring

Charring experiments on modern woods show that there are a number of distinctive changes which occur with increasing temperature (Scott and Jones 1991). Little charring takes place at temperatures less than 200°C.

Depending on the plant material, at between 270 and 320°C the middle lamellae of the cell walls fuse with the main cell walls and become homogenized (Fig. 3.2.3.1g–i). Above this temperature the walls become increasingly brittle and eventually crack and disintegrate between 600 and 1000°C. Another feature of charcoal is that it displays high reflectance when seen in polished blocks in reflected light under oil (Scott 1989). Experiments have shown increasing reflectance with increasing temperature. The charring process has two effects which account for the importance of preservation by fire: (1) it converts the cell wall to nearly pure carbon which makes it more decay resistant; and (2) it preserves the anatomical detail of the plant tissue. When studied under the scanning electron microscope (SEM), charcoal shows outstanding anatomical detail (Fig. 3.2.3.1).

All plant organs may be preserved as charcoal, not only woods (Fig. 3.2.3.1a,b,d,e,g–i) but also leaves (Fig. 3.2.3.1j–l), flowers (Fig. 3.2.3.1c), and pollen organs (Fig. 3.2.3.1f). Large plant fragments tend to fracture and most charcoal fragments are less than 1 cm^3 (Scott 1989). The macroscopic features of charcoal, together with its small size, have led to it being overlooked by geologists and palaeontologists. Macroscopically it can be distinguished from coalified plant tissues not only by its size but also by its lustre and its fine anatomical detail, as seen under the hand lens. These charred organs may be transported by wind or water. In water the charcoal initially floats but eventually becomes waterlogged. Experiments have shown that the time taken to waterlog charcoal depends not only on the plant organ and species but also on the charcoal formation temperature. Charcoal becomes entrained in bedload sediment at moderate current velocities but may, in some cases, stick to bottom muds.

Fossil charcoal

Fossilized charcoal is also known as fusain (Scott 1989). This is one of the coal lithotypes defined by Marie Stopes and is recognized not only by its shape and silky lustre but also, when rubbed with a finger, by its fine black dust. Fusain is common in many ancient terrestrial sediments, as well as in marine rocks. As SEM studies demonstrate, not only can fine internal anatomical details be observed, but also detailed external morphology (Fig. 3.2.3.1). In some cases charring may also preserve ephemeral structures, such as flowers, which often decay rapidly under normal circumstances. The earliest extensive fossil charcoal deposits are of Early Carboniferous age. In the Carboniferous, fossil charcoal deposits are widespread in a variety of sedimentary settings, from braided channel sands to floodplain silts and lowland mires (coals), as well as nearshore marine sediments (Scott and Jones 1994). Fires had a profound effect on these and later terrestrial ecosystems, causing enhanced erosion and deposition and disrupting food chains (Falcon-Lang 1998). Plant material preserved as fusain has been widely studied and many newly discovered plants have been preserved in this way, including the earliest conifer (Fig. 3.2.3.1j,k).

Fossil charcoal is equally common in many younger deposits, including Jurassic, Cretaceous, and Tertiary rocks. For example, braided river sands from the Yorkshire Jurassic Moor Grit contain abundant fossil charcoal, as do coeval sands in the North Sea. Here, much of the fossil charcoal is of wood, but fine, non-marine silts from the Wealden (Lower Cretaceous) of the Isle of Wight contain abundant fern frond fragments (Scott 1989). There is evidence of fire both in the latest Cretaceous and in the earliest Tertiary, based upon the occurrence of charcoal, from many sites. Identifying a global fire at the boundary, as has been claimed, may therefore prove difficult. Of particular significance is the occurrence of small charcoalified flowers in the Upper Cretaceous which have yielded excellent anatomical data and have been useful in the reconstruction of early angiosperm evolution and the development of pollination mechanisms (Fig. 3.2.3.1c).

Implications and consequences of fires in the fossil record

Most geologists and palaeontologists discard fossil charcoal (fusain) as being of little interest—or worse, do not even record its presence. Such material may not only be beautifully preserved but may also signify the occurrence of wildfires, which could have affected erosion/depositional regimes and ecosystem dynamics; it can also provide data on ancient climate and weather systems (Jones and Chaloner 1991). From studies of erosion/depositional cycles following recent fires in several parts of the world, it has been shown that erosion, and hence deposition, may increase up to 30-fold following a major fire. Studies in Yellowstone National Park show that alluvial fans aggrade during periods of frequent fire-related sedimentation events. Such fires may also record drought events and hence record data on weather and climate. Some of the charcoal may also preserve growth rings which may provide extra climatic data. How often is an influx of sediment into a basin considered to be the result of an uplift/erosion cycle rather than a fire-related event? Fire frequency and intensity and its change over time may offer insights into weather patterns and climate change. There have, as yet, been few such studies in the fossil record.

The concentration of atmospheric oxygen controls the initiation and spread of wildfire. The widespread

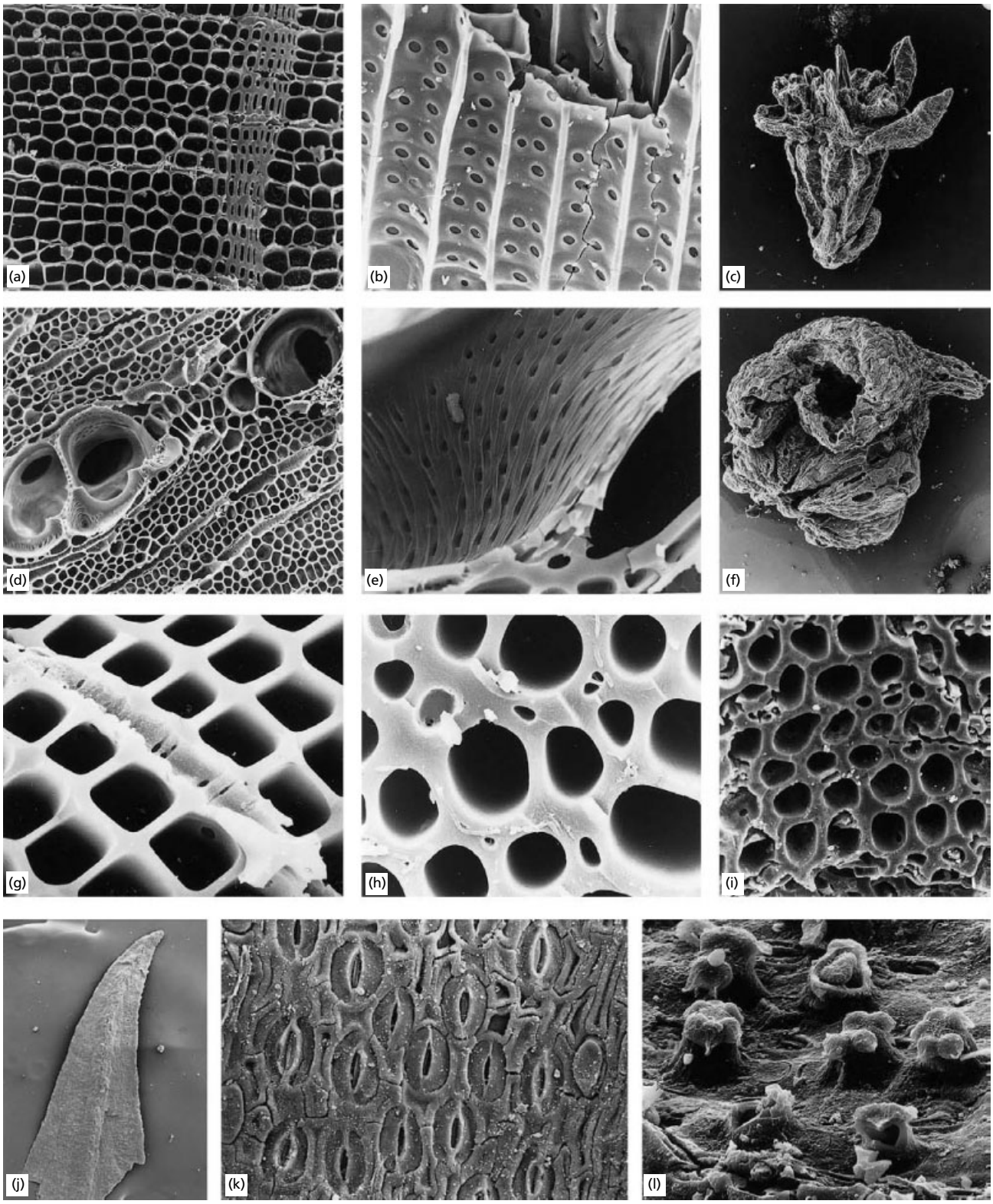

Fig. 3.2.3.1 Scanning electron micrographs of fossil and modern charcoal. (a,b) Taxodiaceous conifer wood, Pliocene, Piedmonte, Italy; (a) transverse section showing growth ring, ×150; (b) detail of longitudinal section showing pitting in tracheid wall, ×350. (c) Flower, *Scandianthus*, Upper Cretaceous, Scania, Sweden, ×30. (d,e) Angiosperm wood charcoalified by hot ash fall, Montserrat; (d) transverse section showing tracheids and vessels, ×180; (e) detail of vessel end plate showing perforations, ×1000. (f) Pteridosperm pollen organ, Lower Carboniferous, Scotland, ×20. (g) Modern charcoalified wood (by wildfire) showing homogenized cell walls, ×1000. (h) Modern charcoalified wood (by hot ash) showing homogenized cell walls, ×1500. (i) Fossil charcoalified wood showing homogenized cell walls, Wealden, Lower Cretaceous, Isle of Wight, ×1000. (j,k) Charcoalified conifer leaf (*Swillingtonia*), Upper Carboniferous, Yorkshire; (j) whole leaf, ×30; (k) detail of stomata, ×360. (l) Leaf surface of *Cordaites* showing rows of glandular hairs between rows of stomata, Upper Carboniferous, Yorkshire, ×800.

occurrence of fire in the fossil record implies oxygen concentrations in the atmosphere of at least 15%. It has also been shown that when oxygen concentrations exceed 35% wet plants might burn and never be extinguished. It has been suggested that during the Carboniferous oxygen levels may have been as high as 30%, which would have enhanced the likelihood of frequent high temperature fires. The abundance of charcoal (fusain) in Carboniferous coals may be a result of these high concentrations of atmospheric oxygen.

It is now clearly established that fire has played an important role in many terrestrial ecosystems over the past 325 million years, and it is important for geologists to consider the consequences in their terrestrial ecosystem models.

References

Crutzen, P.J. and Goldammer, J.G., eds. (1993) *Fire in the environment: the ecological, atmospheric and climatic importance of vegetation fires*. Dahlem workshop reports. Environmental Science Research Reports no. 13. John Wiley, Chichester.

Falcon-Lang, H. (1998) The impact of wildfire on an Early Carboniferous coastal environment, North Mayo, Ireland. *Palaeogeography, Palaeoclimatology, Palaeoecology* **139**, 121–138.

Jones, T.P. and Chaloner, W.G. (1991) Fossil charcoal, its recognition and palaeoatmospheric significance. *Palaeogeography, Palaeoclimatology, Palaeoecology* (*Global and Planetary Change section*) **97**, 39–50.

Rundel, P.W. (1981) Fire as an ecological factor. In: O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler eds. *Physiological plant ecology. 1. Response to the physical environment*, pp. 501–538. Springer-Verlag, Berlin.

Scott, A.C. (1989) Observations on the nature and origin of fusain. *International Journal of Coal Geology* **12**, 443–475.

Scott, A.C. (2000) The Pre-Quaternary history of fire. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **164**, 281–329.

Scott, A.C. and Jones, T.P. (1991) Microscopical observations of recent and fossil charcoal. *Microscopy and Analysis* **25**, 13–15.

Scott, A.C. and Jones, T.P. (1994) The nature and influence of fire in Carboniferous ecosystems. *Palaeogeography, Palaeoclimatology, Palaeoecology* **106**, 96–112.

3.2.4 Role of Microbial Mats

J.-C. GALL

Introduction

Microbial mats are thin laminated ecosystems dominated by bacteria and often with associated fungi, algae, or protozoans. Prokaryotic cyanobacteria form the key component of most of these mats today, producing cohesive viscous layers that vary in thickness from a few millimetres (biofilms) to a metre (microbial mats *sensu stricto*). They occur in a huge variety of environments, including intertidal flats, thermal springs, Antarctic lakes, hypersaline lagoons, and arid deserts. In water bodies, they proliferate on the bottom (benthic mats), at the chemocline, or on the surface (floating mats). They are recorded in the course of Earth history from 3.5 billion years ago and represent the earliest remnants of life on the planet (see Section 1.1.3).

Biological properties

Diverse metabolic activity

Microbial mats incorporate a high diversity of microorganisms and therefore a huge variety of metabolisms. Phototrophic organisms (cyanobacteria, purple sulphur bacteria, algae) are found alongside chemotrophic (sulphide-oxidizing bacteria) or heterotrophic (cellulolytic bacteria, fungi) species. Aerobic cyanobacteria can occur in the immediate vicinity of anaerobic organisms (sulphate-reducing bacteria). Because of the variety of microorganisms interacting in microbial mats, the ecosystem acts as a superorganism, with a global geochemical balance. The tiering of communities in intertidal environments is typical from this point of view. In the North Sea, for instance, multicoloured sands consist of layered mats which exhibit a vertical stratification of different communities of microorganisms: a greenish, 1-mm thick top layer of cyanobacteria and diatoms, above a thin pink layer of colourless and purple sulphur bacteria, which overlies a black sandy layer with iron sulphide, controlled by sulphate-reducing bacteria. The organic matter produced by the phototrophic organisms is broken down by anaerobic bacteria; sulphide is oxidized by sulphur bacteria. Measurements with microelectrodes reveal steep and fluctuating gradients of oxygen and sulphide within the chemical microenvironment of the mats (Gerdes and Krumbein 1987). Vertical growth of the microbial mats reaches several millimetres per year.

High proliferation capacity

Many bacteria have the ability to adapt their metabolism to changes in the prevailing environment, or to modify their genetic make-up by exchanging molecules of extrachromosomal DNA. This dual plasticity confers on the microbial world an extraordinary capacity to proliferate quickly in unoccupied media. For example, in tropical waters biofilms develop on fish carcasses within a couple of hours.

Intense production of mucilage

Microorganisms involved in the construction of mats (e.g. cyanobacteria, diatoms) excrete a high amount of mucilage, composed mainly of polysaccharides. This is responsible both for binding cells and sediment particles together and for sealing geochemical microenvironments, thereby limiting the diffusion of chemical elements.

Food supply

Several bacteria produce toxic compounds which inhibit the settlement of other fauna. Nevertheless, microbial mats constitute an attractive food supply for a variety of grazing animals (annelids, gastropods, crustaceans, fishes, etc.). This explains why microbial mats today are restricted to extreme environments which exclude most higher species.

Physical behaviour

Trapping of sediment particles

The physical behaviour of a microbial mat resembles that of a supple tissue. This results from its net-like structure, generated by filamentous organisms (particularly cyanobacteria but also actinomycetes and sulphate-reducing bacteria). Detrital particles or microorganisms are easily trapped in the meshes of the net and fixed by mucilage (Figs 3.2.4.1 and 3.2.4.3b).

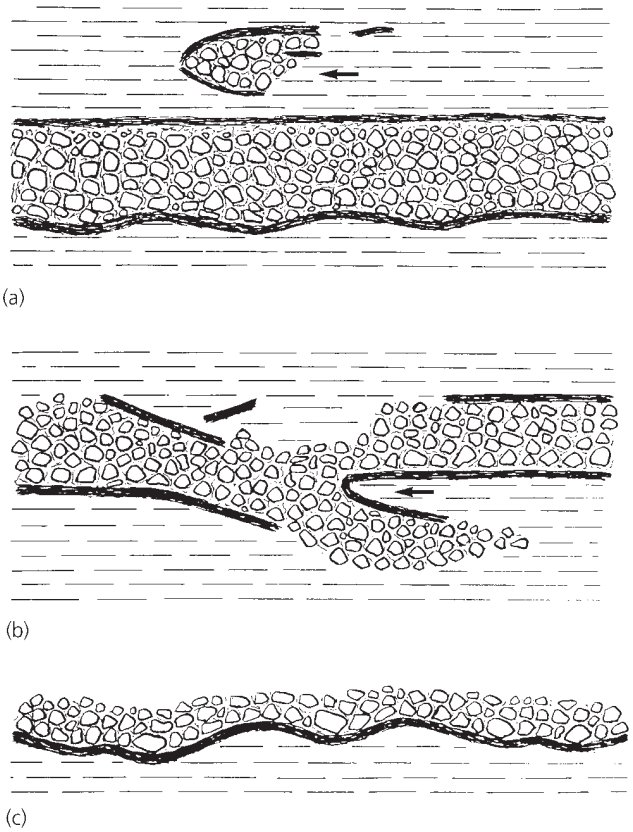

Fig. 3.2.4.1 Physical behaviour of biofilms (dark texture) shown in thin sections. (a) Trapping of detrital particles and fragmentation (intraclast). (b) Breaking and folding (arrow). (c) Supple deformation. Shale of the Grès à Voltzia Formation (Upper Buntsandstein, Vosges, France).

Biogenic sediment stability

The impact of microbial mats on sedimentation was long underestimated. Their filamentous framework and abundant mucilage bind and stabilize sedimentary particles and inhibit the mobilization of sediment by currents. Tidal flat sands settled with mats or biofilms are 3–20 times more resistant to erosion than uncolonized areas (Krumbein *et al.* 1994). Such a sediment-stabilizing capacity accounts for the preservation of delicate sedimentary and biogenic structures in the rock record (e.g. lithographic limestones). Microbial mats are nevertheless easily warped and disrupted; fragmentation is controlled by their filamentous framework, which results in the production of polygonal pieces.

Chemical impact

Biomineralization

A very important aspect of microbial communities concerns their involvement in mineralization processes (Briggs and Kear 1993). Their role, for instance, in carbonatogenesis has been repeatedly demonstrated in the laboratory. Precipitation of calcium carbonate is first induced actively in the bacterial membranes. A passive phase follows, during which bacterial bodies are coated by a calcified shell. Microorganisms also contribute to the generation of apatite, as well as several different kinds of iron mineral (pyrite, siderite, magnetite, etc.). Concentrations of elements like lead, copper, manganese, and gold are linked to the activity of microbial mats. They are favoured by mucilage production which restricts ion exchange with the prevailing environment.

Anoxia

Anoxic conditions become established on the bottom of lakes or oceans when the water column is temporarily or permanently density-stratified. Oxygen-deficient conditions are often assumed to favour the development of microbial mats. In fact, the production of abundant

mucilage restricts chemical exchanges between sediment and the water column; such conditions prevent the settlement of benthic animals and favour the preservation of organic matter, as is the rule for black shales.

Recognition in ancient sediments

Biogenic laminations

The growth of microbial mats is controlled by such physical and chemical factors as temperature, light, salinity, and moisture. Seasonal and secular rhythmic variations of microbial activity contribute to the layered structure of the sediments. The resulting texture consists of biolamination where dark laminae, less than 1 mm in thickness and enriched in bacterial organic matter, alternate with light laminae, mostly built up by detrital particles. Similar processes are well documented in stromatolites formed by the lithification of microbial mats. In thin sections, the occurrence of biofilms is easily detected because the filamentous framework retains the detrital particles.

Microscopic structures

The filaments which contribute to the construction of microbial mats are often fossilized and identifiable in thin section or under the SEM (Fig. 3.2.4.3c). The impact of microbial activity on mineral genesis, as demonstrated in the laboratory, is more difficult to recognize in ancient rocks because of obliteration by diagenetic processes. Nevertheless, in some cases, the arrangement of crystals (e.g. dolomite) is obviously linked to the filamentous framework of microbial mats.

Macroscopic structures

In many cases the mats were distorted during sedimentation and exhibit structures typical of, for instance, sliding down slopes (wavy or torn structures) or disruption and fragmentation by currents (Figs 3.2.4.1 and 3.2.4.3d). Fragments of reworked mats can be recognized by their polygonal shape (Gall 1995).

Role in taphonomy

Trapping of organisms

The filamentous network of microbial mats and their abundant production of mucilage favours the trapping not only of sediment particles but also of small organisms. This leads to the capture of planktic species as well as animals dead on the water surface. The organisms are then carried down to the floor of the aquatic environment as the mat sinks to the bottom. If bottom conditions are anoxic, they can be fossilized. Many localities where fossil insects are well preserved in finely laminated sediments probably rely on such a mechanism. In fact, insect carcasses can drift for a long time on the water surface, where feeding by necrophagous animals provokes their disarticulation. This is why fossil insects are often preserved incomplete. The fossilization of complete bodies is possible through trapping by floating microbial mats and rapid sinking to the bottom.

Soft tissue preservation

During decay, labile tissues such as skin, muscles, and internal organs decompose very rapidly. In order to fossilize, they must be replaced by authigenic minerals. Laboratory experiments on shrimp carcasses have shown that bacterial activity induces replacement by calcium phosphate within 2–4 weeks (Briggs and Kear 1993). Such a process accounts for the phosphatized skin and fins of ichthyosaurs recovered from various European Liassic black shales, and for the remarkable fishes from the Santana Formation (Cretaceous), Brazil, in which muscles and gills are preserved.

Soft tissue can also be replaced by siderite. Particularly spectacular from this point of view are the fossils preserved in the bituminous shales of Messel (Germany), a lacustrine Fossil-Lagerstätte of Eocene age. Many vertebrates, including fishes, amphibians, reptiles, birds, and mammals, exhibit the outline of soft parts such as skin and muscles. For example, scanning electron microscopy has revealed that the body outline of a bat is completely covered by masses of lithified bacteria (Franzen 1985). Pyrite induced by bacterial metabolic activity forms too late in the decay process to preserve the microscopic structure of soft tissues.

The microbial shroud

In shallow-water environments, the rapid growth of microbial mats protects carcasses against decay and destruction by scavengers (Fig. 3.2.4.2). Further thickening of the mats hinders penetration by burrowing animals which would otherwise disarticulate the buried skeletons. Production of toxic compounds reinforces this barrier. This explains why good articulated tests and skeletons occur in the Toarcian black shales of Holzmaden (Germany), despite evidence of their orientation by strong currents. The sealing effect of the mats is also responsible for preservation of ephemeral sedimentary structures, such as footprints and locomotion tracks. Lithographic limestones from the Kimmeridgian of Cerin (France), with their tracks of turtles and dinosaurs, are a famous example of the role of microbial mats in taphonomy (Fig. 3.2.4.3a) (Gall 1998).

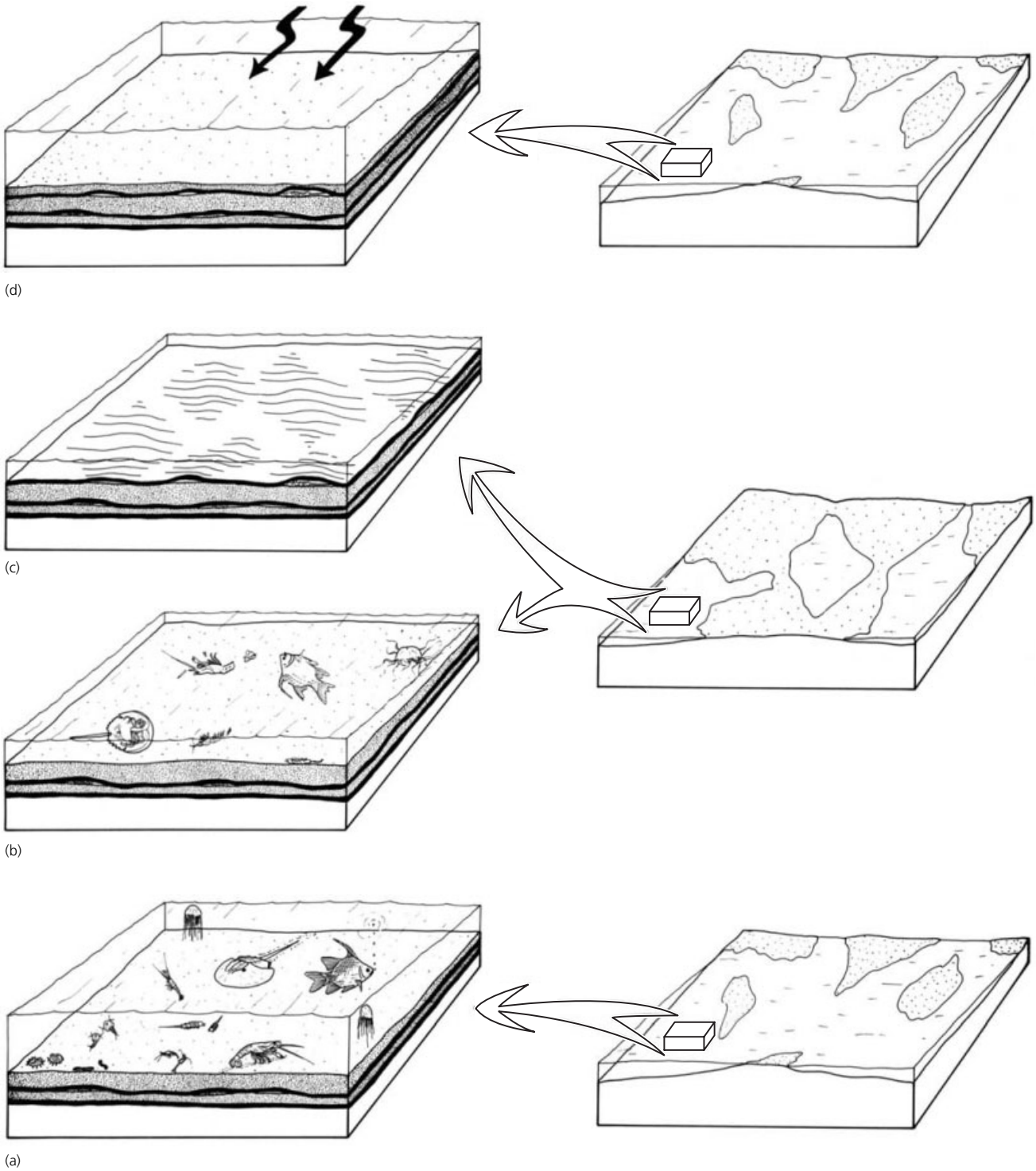

Fig. 3.2.4.2 Taphonomic history of a fossiliferous shale of the Grès à Voltzia Formation (Upper Buntsandstein, Vosges, France). (a) Proliferation of an aquatic fauna. (b) Mass mortality resulting from anoxic water body. (c) Spreading of a microbial mat (dark lamina). (d) New supply of detrital material sealing the mat and the carcasses.

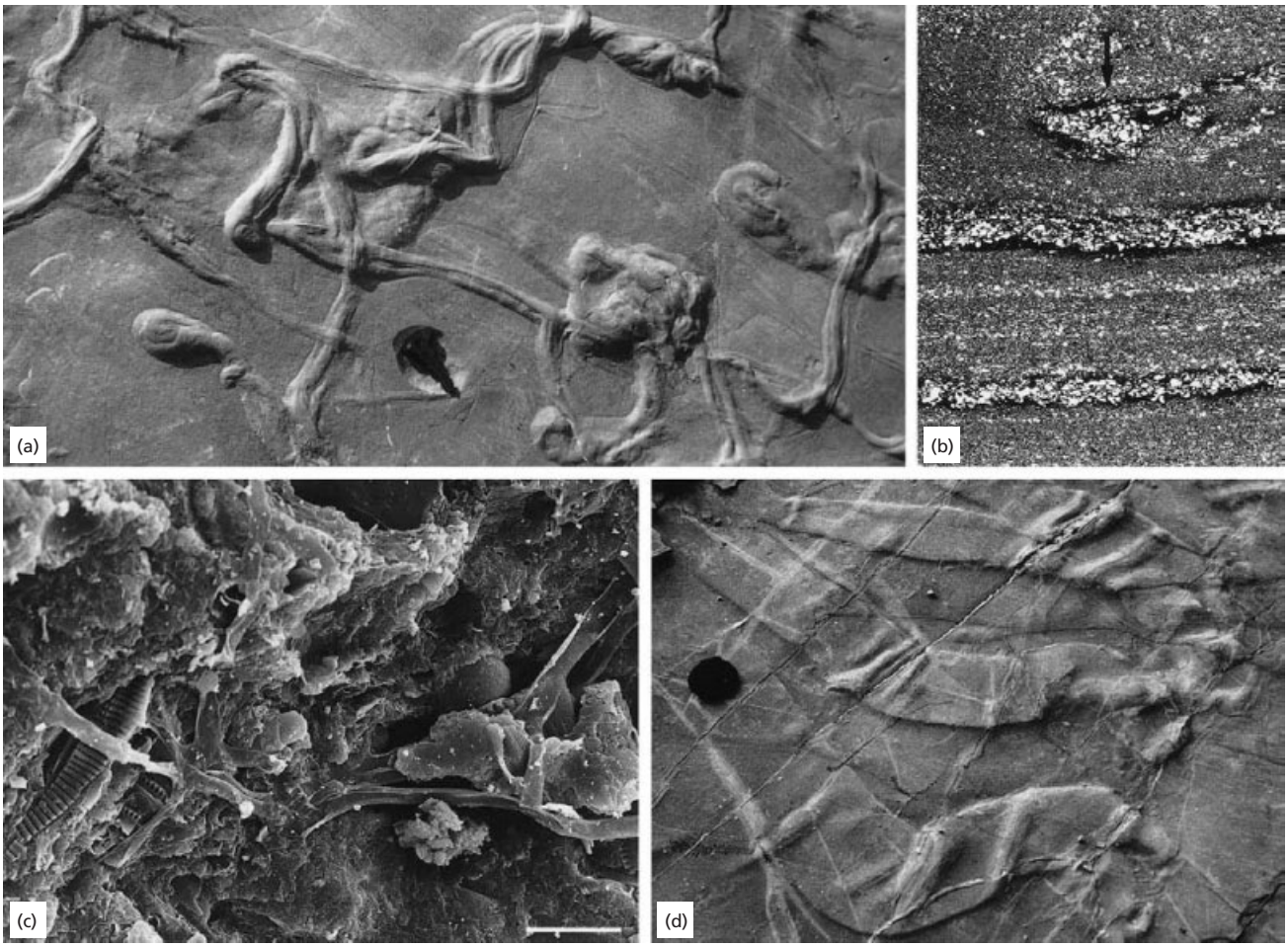

Fig. 3.2.4.3 (a) Filamentous texture (cyanobacteria or algae), revealed by dislocation of a microbial mat on the surface of a lithographic limestone bed; Upper Kimmeridgian, Cerin (Jura, France); key, 4 cm long. (b) Light micrograph of thin section showing silt particles trapped in a biofilm (dark texture), and preservation of an intraclast (arrow); shale of the Grès à Voltzia Formation (Upper Buntsandstein, Vosges, France); width of photograph, 10 mm. (c) SEM micrograph showing network of filamentous microbes (actinomycetes?) in a lacustrine diatomite; Oligo-Miocene, Anatolia (Turkey); scale 10 µm. (d) Torn and folded microbial mat on the surface of a lithographic limestone bed; Upper Kimmeridgian, Cerin (Jura, France); camera lens cover, 5.5 cm. (a,c,d, From Gall 1995.)

Conclusion

The role of microbial mats in taphonomy is threefold: (1) to preserve sediment against erosion and consequently to retain such ephemeral biogenic features as footprints, tracks, and other markings; (2) to protect carcasses against decay and scavengers and to ensure the preservation of articulated shells and skeletons; and (3) to create particular microenvironments favourable to mineralization, where the fossilization of soft tissue morphology may occur.

References

Briggs, D.E.G. and Kear, A.J. (1993) Fossilization of soft-tissue in the laboratory. *Science* **259**, 1439–1442.

Franzen, J.L. (1985) Exceptional preservation of Eocene vertebrates in the lake deposit of Grube Messel (West Germany). In: H.B. Whittington and S. Conway Morris, eds. Extraordinary fossil biotas: their ecological and evolutionary significance. *Philosophical Transactions of the Royal Society of London B* **311**, 181–186.

Gall, J.C. (1995) Biofilms and microbial mats: their contributions to sediment genesis. *Comptes Rendus de l'Académie des Sciences Paris Serie IIa* **321**, 823–835.

Gall, J.C. (1998) *Paléoécologie: paysages et environnements disparus*. Masson, Paris, Milan and Barcelona.

Gerdes, G. and Krumbein, W.E. (1987) *Biolaminated deposits*. Lecture Notes in Earth Sciences. Springer-Verlag, Heidelberg.

Krumbein, W.E., Paterson, D.M. and Stahl, L.J., eds. (1994) *Biostabilization of sediments*. Bibliotheks und Informationssystem der Universitat Oldenburg, Oldenburg.

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3.2.5 Bioimmuration

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Introduction

Bioimmuration is preservation due to organic overgrowth. The term has been applied to both the process and the product. Bioimmuration is an important yet scarcely studied mode of fossilization which is capable of preserving sessile organisms without mineralized hard parts in ordinary depositional settings. A simple example of bioimmuration is the formation of an imprint (external mould) of a soft-bodied hydroid on the shell attachment area of an oyster which shared the same substratum and overgrew the hydroid. Such overgrowth is a routine result of competitive interactions for living space between organisms which encrust hard surfaces in the sea. Therefore, bioimmuration is rife.

Types and processes of bioimmuration

Different kinds of bioimmurations can be classified according to: (1) the spatial and dynamic relationships between immurer (organism responsible for overgrowth), immuree (overgrown organism), and substratum; and (2) prevailing taphonomic and diagenetic factors (Fig. 3.2.5.1). In the first case, it is useful to distinguish between epibiont bioimmurations, substratum bioimmurations, and bioclaustrations. Epibiont bioimmurations are usually three-component systems: a substratum is encrusted by both immurer and immuree, as in the example of the hydroid overgrown by the oyster mentioned above. It is important to note that epibiont bioimmurations, especially extensive bioimmurations of colonial organisms, may not correspond to the appearance of the overgrown organism at any one moment during its lifetime. This is because the gradual process of overgrowth produces a fossil which is integrated through time: different parts of the organism become 'encapsulated' at different times. Substratum bioimmurations are two-component systems, comprising an immurer which grows upon and bioimmures an organic substratum, as, for example, when a blade of seagrass is bioimmured by an oyster which is using it as a substratum. Bioclaustrations are similar to the last but involve active, mutual intergrowth between the immurer and immuree to give what has been termed an embedment fossil or a pseudoboring. The term was first coined (Palmer and Wilson 1988) for the ichnogenus *Catellocaula* which occurs embedded within Ordovician bryozoans. Whereas epibiont and substratum bioimmurations are body fossils, the more dynamic relationship between immurer and immuree means that bioclaustrations are better regarded as trace fossils. Indeed, many bioclaustrations merge into borings if intergrowth with a living host follows the initial penetration by the boring animal (e.g. boring bivalves inhabiting domiciles in growing corals).

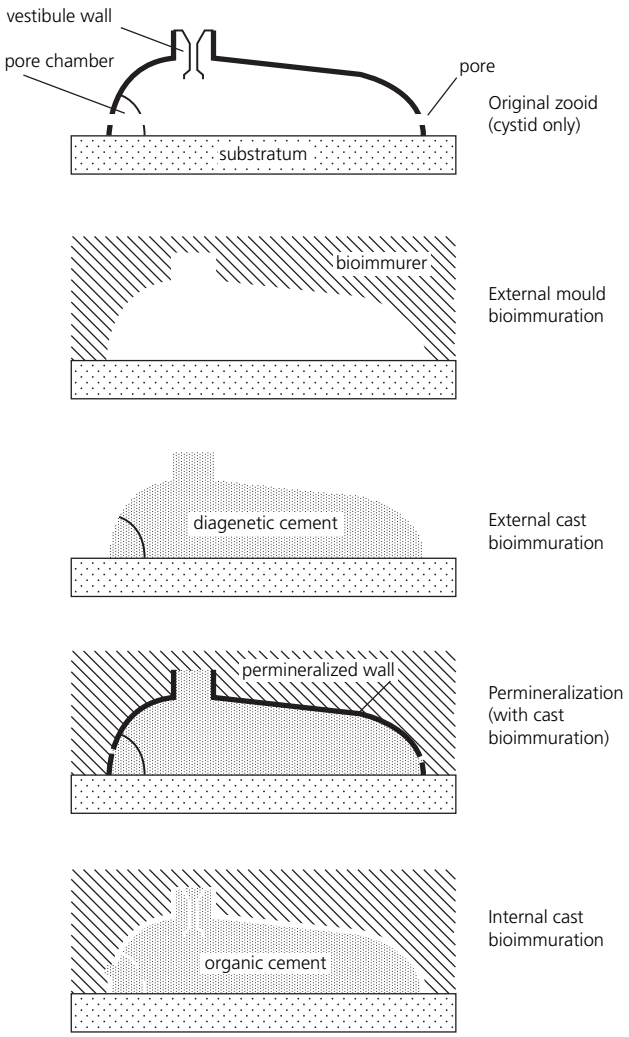


Fig. 3.2.5.1 Schematic diagram showing different modes and styles of bioimmuration using a ctenostome bryozoan zooid (sectioned longitudinally) as the immuree. In all cases, the zooid body walls are indicated in solid black, the substratum of encrustation by coarse stippling, the overgrowing (bioimmuring) organism by diagonal hatching, and cement infill by fine stippling. The immurer has been removed from the external cast bioimmuration to depict better the way that such fossils are normally found as casts of diagenetic cement adhering to surfaces of hard substrates.

The completeness and fidelity of bioimmured fossils can be influenced profoundly by the following taphonomic and diagenetic factors: (1) the amount of defor-

mation or breakage during overgrowth; (2) the rapidity of overgrowth; (3) whether the immuree was dead or alive when overgrown; (4) whether the immurer had a mineralized cement layer or could produce a biogenic cement infill; and (5) the presence of a diagenetic mineralized infilling, its composition, time of formation, and subsequent history. Erect parts of bioimmured epibionts may be pushed over in the direction of overgrowth and flattened against the substratum. It is essential that this is taken into account when inferring the original morphology of the immuree. Fortunately, the correspondence between the orientation of the immuree and the local growth direction of the immurer enables originally erect structures to be recognized (Fig. 3.2.5.2a). Immurers may grow sufficiently rapidly that small solitary epibionts and individual zooids of colonial epibionts are completely smothered before they have decayed significantly. In the case of some substratum bioimmurations, the extreme size contrast between the immurer and the immuree (e.g. mangrove oysters cemented to the roots of mangrove trees) means that overgrowth of the immuree is commonly non-fatal.

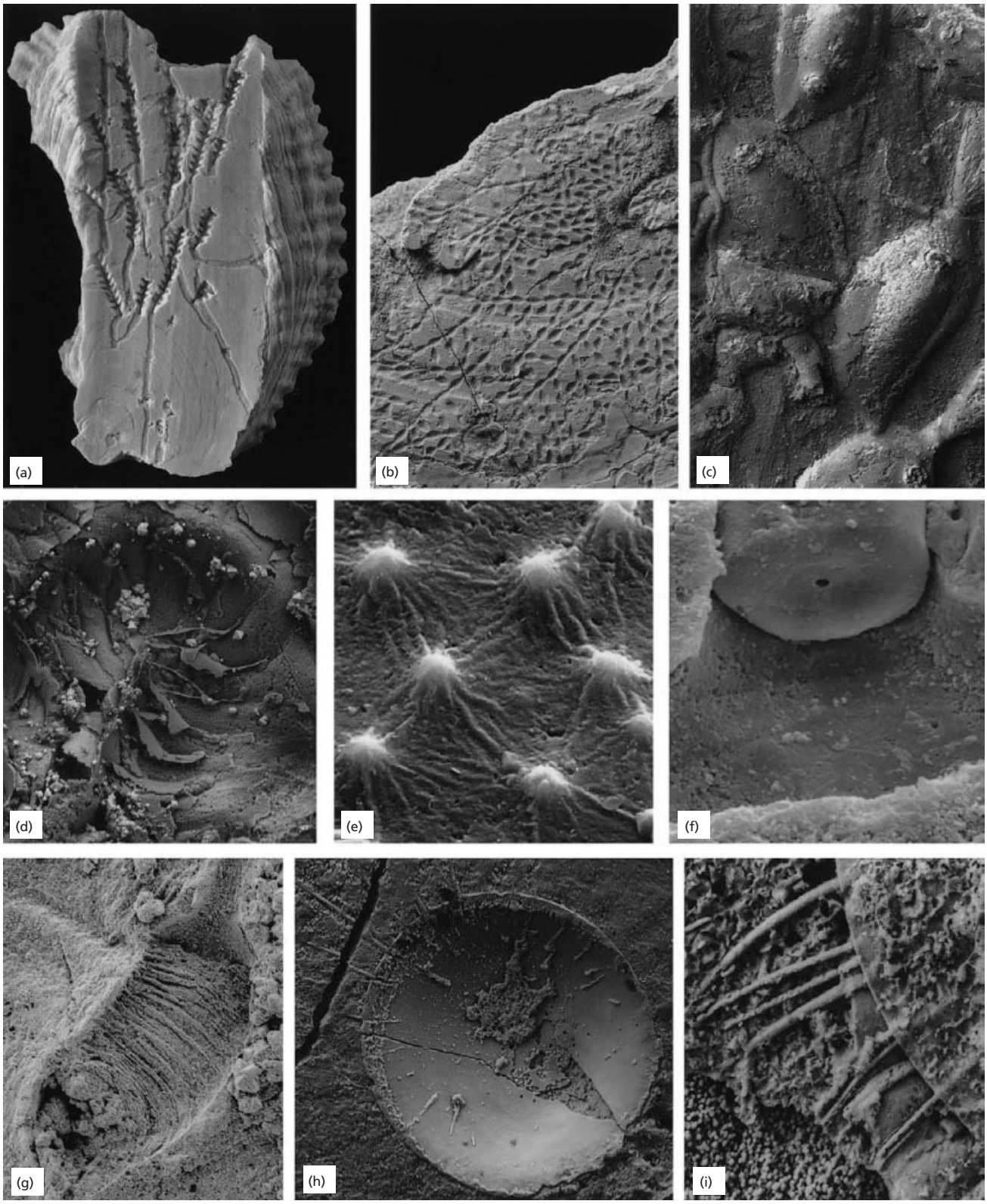
The simplest bioimmurations are external moulds (Fig. 3.2.5.2a,b). The fidelity of the mould depends partly on the method used by the immurer to adhere to the substratum. Immurers having a thick organic layer forming the 'glue' produce poorer quality moulds than immurers with a mineralized cement layer because fine-scale surface features of the overgrown organism may lose fidelity on transmission to the skeleton. Immurers with a mineralized cement layer include encrusting bivalves which precipitate an extrapallial cement of calcium carbonate between the thin organic periostracum and the substratum, encapsulating overgrown organisms and moulding their shapes with great precision.

Cast bioimmurations (Fig. 3.2.5.2c) often provide more morphological information than moulds. Casting can be accomplished in two different ways. Some immuring organisms secrete a biogenic cement which is capable of pervading the interior of the overgrown organism, hardening within and leaving an internal cast of the immuree. For example, serpulid worms manufacture a slurry of mucus and calcium carbonate which they paste on to the growing tube, solidifying when it contacts sea water. This slurry can seep into the body cavities of overgrown organisms: the stolons of a soft-bodied Jurassic bryozoan colony (Fig. 3.2.5.2f), for example, are filled by serpulid biomineral as far as transverse partitions (septa) which halted further progress of the slurry (Todd 1994).

More commonly, however, casting of bioimmured organisms occurs during diagenesis, resulting in external casts which usually consist of calcite, pyrite, or a combination of the two (Fig. 3.2.5.2c). Diagenetic calcite is a late stage precipitate which often partly or completely infills the epibiont mould between substratum and immurer. The resultant calcite cast frequently remains adherent to the surface of the substratum when the immurer is removed, and can be mistaken for an originally skeletonized epibiont. Bioimmuration provides an ideal microenvironment for the formation of pyrite: locally elevated sulphide levels produced during decay of the immuree rapidly results in iron sulphide supersaturation and precipitation. Early diagenetic pyrite in cast bioimmurations is typically framboidal, whereas euhedral and equant pyrite crystals are products of late stage diagenesis.

Soft tissues may also be permineralized in bioimmured fossils. Organic cuticles of bioimmured bryo-

Fig. 3.2.5.2 (*Facing page*) Bioimmured fossils. (a) External mould bioimmuration of the hydroid ?*Dynamena* on the attachment area of the oyster *Cubitostrea*; the hydroid colony grew on a living sea-grass leaf and the erect branches were pushed over and immured by the upwardly growing oyster; Middle Eocene, Paris Basin, France; ×3. (b) Part of the attachment area of a large *Gryphaea* with an external mould bioimmuration of an extensive colony of the ctenostome bryozoan *Simplicidium*; Upper Jurassic, Normandy, France; ×4. (c) Composite internal/external cast bioimmuration of *Simplicidium* zooids preserved in calcite (dark) and pyrite (light); stolon on far left belongs to an overgrowing hydroid colony; Upper Jurassic, Normandy, France; ×55. (d) Creeping tube of the pterobranch *Rhabdopleura* preserved as an external mould bioimmuration; zigzag suture contains periderm remnants; Upper Jurassic, Normandy, France; ×140. (e) Calcite permineralized cuticle of a ctenostome bryozoan, bioimmured by the oyster *Deltoideum*, showing tiny (1.5 µm diameter) pustules; Upper Jurassic, Lincolnshire, England; ×4000. (f) Branching stolon of the ctenostome bryozoan *Buskia* preserved as an internal cast bioimmuration; septum at junction between branches of stolon has halted further ingress of carbonate-charged slurry secreted by an immuring serpulid; minute hole is an external mould of the bryozoan funiculus which connected the living zooids; Upper Jurassic, Normandy, France; ×1400. (g) Wrinkled socket (basal cylinder) of upright zooid of the entoproct *Barentsia* which has been pushed over, compressed, and immured by the oyster *Deltoideum*; the entoproct cuticle is preserved as a thin phosphatic lining within the external mould; Upper Jurassic, Lincolnshire, England; ×220. (h) Dorsal valve of the inarticulate brachiopod *Discinisca* preserved within the attachment area of the overgrowing oyster *Deltoideum*; permineralized setae and traces of the mantle canals are visible; Upper Jurassic, Lincolnshire, England; ×120. (i) Detail of permineralized setae of a bioimmured *Discinisca*; setae emerge from between the ventral valve (visible top right) and the overlapping dorsal valve; Upper Jurassic, Oxfordshire, England; ×340. All specimens are in the collections of The Natural History Museum, London. (a,b) Photomicrographs; (c,d,h,i) back-scattered scanning electron micrographs of uncoated specimens; (e–g) secondary electron scanning micrographs of coated specimens.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(h)
(i)

zoans and entoprocts can be permineralized by calcite (Fig. 3.2.5.2e) or apatite (Fig. 3.2.5.2g) which may preserve micrometre-scale details. In summary therefore bioimmurations range from straightforward external moulds to complex internal casts with associated permineralization which can provide a wealth of anatomical information.

Discovering bioimmurations

The search for bioimmurations in the fossil record, and interpretations of their distribution through geological time, is aided by a knowledge of the principal bioimmuring organisms. These comprise three groups: cemented bivalves (including true oysters), serpulid worms, and calcareous bryozoans. Examination of naturally exposed attachment areas in fossils (Fig. 3.2.5.2a,b) belonging to these groups is the easiest way to find bioimmurations. Attachment areas may be readily visible if the bivalve, serpulid, or bryozoan originally encrusted a soft-bodied organic substrate that subsequently decayed, or an aragonite shell that dissolved during diagenesis. Alternatively, it is often possible to flake fossil encrusters off their substrates, revealing epibiont bioimmurations as moulds on the attachment area and/or as casts on the surface of the substrate (Fig. 3.2.5.2c). Such specimens are usually of higher quality than those exposed naturally.

Cemented bivalves and serpulid worms are largely post-Palaeozoic groups. The absence or rarity of earlier examples of these immurers is a major reason why so few Palaeozoic bioimmurations have been reported, together with the generally greater cementation and diagenetic alteration of Palaeozoic fossils. Nevertheless, the abundant stenolaemate bryozoans of the Palaeozoic, as well as other cemented groups such as cornulitid 'worms' and certain brachiopods, corals, and stromatoporoids, offer scope for considerably enlarging the meagre number of Palaeozoic bioimmurations documented so far.

Bioimmured groups

Important examples of sessile organisms preserved by bioimmuration include algae, sea-grasses, hydroids, ctenostome bryozoans, entoprocts, pterobranchs, and brachiopods, as well as other groups (reviewed by Taylor 1990a). In addition, there are many bioimmurations which, through lack of detail or obvious modern analogues, cannot be assigned readily to a taxon.

Examples of bioimmured marine plants are found in the Upper Cretaceous Chalk-Tuff of the Maastricht region, Holland (Voigt 1966), and the Middle Eocene of the Paris Basin (Fig. 3.2.5.2a). Substratum mould bioimmurations in the Chalk-Tuff usually resulted from the overgrowth of stems of algae and leaves of sea-grasses by cyclostome bryozoans, although oysters, serpulids, and even foraminifers were occasional immurers. Bioimmurations of sea-grass leaves preserve the patterns of the epidermal cells and the veins, providing unequivocal evidence of an early sea-grass community.

Many of the bioimmured plants from the Chalk-Tuff supported an epiphytic biota of hydroids and ctenostome bryozoans, which are preserved as epibiont mould bioimmurations. Despite their importance in modern epibenthic communities, hydroids have a scant fossil record because of their non-mineralized, chitinous skeleton. The small size of the zooids in hydroid colonies makes them suitable for bioimmuration—not only can individual zooids be overgrown entirely before decaying but colonies can sustain substantial levels of partial mortality (zooid death) while continuing to live and grow. This is also true of ctenostome bryozoans, another group extensively bioimmured in the Mesozoic (Fig. 3.2.5.2b).

The most spectacular bioimmurations so far recorded are from Jurassic and Lower Cretaceous clays in northern Europe, particularly the Upper Jurassic Oxford and Kimmeridge Clays of England and their equivalents in Normandy (Todd 1993). Here, the large oysters *Gryphaea* and *Deltoideum* served as substrates for a variety of soft-bodied and thinly mineralized animals which are commonly bioimmured by other oysters and serpulid worms. Some of the bioimmurations are simple external moulds, but the most informative involve casting and/or permineralization.

A previously unsuspected diversity of ctenostome bryozoans has been recognized, including some consisting of encrusting uniserial chains of zooids (Fig. 3.2.5.2b) and others of ramifying stolons bearing erect or semierect zooids at intervals along their length (Todd 1994). These bioimmured ctenostomes represent the only fossil records of many Recent families. Furthermore, some species have opercula which identify them as stem-group Cheilostomata, providing crucial evidence of the origin of this skeletonized order which dominates modern bryozoan faunas (Taylor 1990b).

The only unequivocal fossils of the Phylum Entoprocta yet described are bioimmurations from the Upper Jurassic (Todd and Taylor 1992). This group of pseudocoelomate metazoans contains about 150 living species of small, sessile suspension-feeders, some solitary, others colonial. The bioimmured Jurassic entoprocts can be assigned to the extant colonial genus *Barentsia*. Colonies were engulfed by the extrapallial cement secreted by the oyster *Deltoideum delta*, and the organic cuticle was subsequently phosphatized. The bioimmurations reveal a system of stolons supporting the tall, erect zooids, with their distinctive basal sockets (Fig. 3.2.5.2g),

rods, and calices, which were pushed over and flattened against the substratum during overgrowth.

Pterobranchs and minute inarticulate brachiopods with preserved setae are also commonly preserved as bioimmurations in the Upper Jurassic clays of England and Normandy. The living pterobranch *Rhabdopleura* has particular palaeontological significance as the closest living relative of graptolites. Fossil *Rhabdopleura* has been known for many years, preserved as highly compressed colonies or small, isolated three-dimensional fragments. In contrast, bioimmured specimens preserve entire colonies comprising zooidal and creeping tubes (Fig. 3.2.5.2d). Details of colony budding pattern can be studied, as well as the black stolon and the fusellar structure of the periderm. Like *Rhabdopleura*, inarticulate brachiopods are seldom recorded from Upper Jurassic clays, yet bioimmuration reveals that shelly substrates were frequently colonized by myriads of the tiny brachiopod *Discinisca*. The fragile chitinophosphatic shells of *Discinisca* are commonly less than 1 mm in diameter. Bioimmured specimens often preserve the long, permineralized setae extending from between the valves of the brachiopod (Fig. 3.2.5.2h,i).

Conclusion

Much remains to be learnt about bioimmuration as a process, and about the variety of organisms that can be fossilized in this way. A major challenge is to find further examples of Palaeozoic bioimmurations, and no work has yet been done in the area of experimental taphonomy. Bioimmuration has already proved to be of immense value in greatly extending the geological ranges of taxa, addressing phylogenetic issues, and revealing the soft-bodied and weakly mineralized organisms present in hard and firm substrate palaeocommunities. In preserving the generally small and sessile inhabitants of hard substrates, Bioimmuration Lagerstätten complement the better-known marine Lagerstätten such as the Burgess Shale and Hünsruck Slate where larger, soft substrate-dwelling organisms predominate. Many marine encrusting communities today are dominated by soft-bodied organisms, yet almost nothing is known about their palaeoecology. There is great scope for examining changes in the composition and ecology of encrusting communities, including patterns of competitive interaction and substrate coverage, through geological time.

References

Palmer, T.J. and Wilson, M.A. (1988) Parasitism of Ordovician bryozoans and the origin of pseudoborings. *Palaeontology* **31**, 939–949.

Taylor, P.D. (1990a) Preservation of soft-bodied and other organisms by bioimmuration—a review. *Palaeontology* **33**, 1–17.

Taylor, P.D. (1990b) Bioimmured ctenostomes from the Jurassic and the origin of the cheilostome Bryozoa. *Palaeontology* **33**, 19–34.

Todd, J.A. (1993) The bivalve shell as a preservation trap, as illustrated by the Late Jurassic gryphaeid, *Deltoideum delta* (Smith). *Scripta Geologica, Special Issue* **2**, 417–433.

Todd, J.A. (1994) The role of bioimmuration in the exceptional preservation of fossil ctenostomates, including a new Jurassic species of *Buskia*. In: P.J. Hayward, J.S. Ryland and P.D. Taylor, eds. *Biology and palaeobiology of bryozoans*, pp. 187–192. Olsen and Olsen, Fredensborg.

Todd, J.A. and Taylor, P.D. (1992) The first fossil entoproct. *Naturwissenschaften* **79**, 311–314.

Voigt, E. (1966) Die Erhaltung vergänglicher Organismen durch Abformung infolge Inkrustation durch sessile Tiere. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **125**, 401–422.

3.2.6 Transport and Spatial Fidelity

L.C. ANDERSON

Introduction

With few exceptions, organic remains are potentially subject to postmortem transport. Agents of transport can be physical (e.g. currents, waves, mass movement) or biological (e.g. bioturbation, predation, hermit crabs). Postmortem movement appears pervasive because fossils are rarely preserved in life position, spatial relations of individual organisms relative to one another typically cannot be reconstructed in fossil assemblages, and instances of long-distance transport have been documented. However, fossil assemblages have long been used to infer palaeoenvironmental conditions. To be reliable palaeoenvironmental indicators, biotic remains by and large must be incorporated into the sedimentary record within their life habitat, and instances of out-of-habitat transport must be readily detectable.

Given these observations, what are the limits of spatial resolution in the rock record? No single answer to this question is possible because spatial resolution varies both with taxonomic group and depositional environment. Fortunately, taxonomic and environmental effects have been documented for most major groups of bioclast-producing organisms and variation in spatial fidelity is, to some extent, predictable. In general, fossil assemblages reflect rather well the local to regional composition of the biota that produced them.

Documenting spatial fidelity

Typically, spatial fidelity is defined as the congruence of a species' organic remains and its habitat (Kidwell and Flessa 1995). The term has also been defined, especially for vertebrates, as the proximity between the place an organism died and the site of final burial (Behrensmeyer and Hook 1992). Spatial fidelity is examined most often by comparing the distributions of living organisms and their dead remains. For example, if life and death assemblages show comparable sample groupings in Q-mode cluster analyses, transport is considered to be insignificant. Another means of evaluating spatial fidelity is to compare death assemblages with environmental parameters. If sample groupings based on taxonomic composition correspond to areas with distinct environmental conditions, transport is considered negligible. Spatial fidelity can also be evaluated by comparing faunal distribution patterns of surface and subsurface bioclast accumulations to determine if faunal heterogeneity in surficial deposits is accurately recorded in subsurface shell beds. In addition, transport can be evaluated by comparing sea-level curves, which track the position of the shoreline over time and space, with distributions of age-dated shells of environmentally restricted estuarine or intertidal species. Transport is inferred for shells whose ages do not fall on the sea-level curve.

Distinguishing indigenous and exotic bioclasts

Recognizing indigenous bioclasts (i.e. those that occur within the habitat of the species forming them) and exotic bioclasts (i.e. those that are transported from their original habitat) is relatively straightforward in modern environments where live communities, death assemblages, and environmental parameters can be evaluated separately. Distinguishing indigenous and exotic bioclasts is more difficult in fossil assemblages, although a number of studies of both modern and ancient sediments have sought to establish and test criteria to detect transported and/or reworked remains (see Kidwell and Flessa 1995). For instance, indigenous assemblages should contain species with similar or overlapping environmental preferences, and transported bioclasts will typically be represented by only a few specimens. However, assemblages that undergo bulk transport may retain their environmental signal. In addition, not all rare species are exotic, and exotic bioclasts may be abundant if indigenous elements have a low preservation potential (e.g. Martin and Wright 1988).

Species habitat preferences can also be compared to the palaeoenvironmental conditions inferred from associated sediments and sedimentary structures in order to evaluate spatial fidelity. Other sedimentological criteria used to recognize indigenous assemblages include the following: (1) assemblages contain bioclasts differing in transport potential (e.g. juveniles and adults); (2) assemblages are not hydraulically equivalent to the associated matrix; (3) assemblages are not associated with sedimentary structures indicative of sediment transport such as normal grading; and (4) assemblages contain bioclasts in life position or with no preferred orientation. None of these criteria is diagnostic, however. Size-selective destruction without transport can occur, and hydraulically mixed assemblages may form during transport if there are multiple sources of bioclasts. In addition, physical or biological mixing without transport can produce graded bedding, and interference effects can prevent bioclasts in dense accumu-lations from assuming a preferred orientation despite transport.

Taphonomic features also have been used to evaluate transport. For instance, in indigenous assemblages bioclasts with equivalent preservation potential (i.e. same mineralogy or microstructure) should show similar types and degrees of taphonomic alteration, and both durable and fragile bioclasts should be present. Transport processes, however, do not produce a characteristic taphonomic signature, and alteration typically reflects taphonomic processes at work in the life habitat of a species. In addition, recently dead delicate carcasses can be transported long distances without damage, and multiple bioclast sources (spatial and/or temporal) can produce assemblages with a mix of durable and fragile bioclasts.

In conclusion, it should be stated explicitly that no single criterion is diagnostic of transport. Therefore, careful examination of the palaeoecological and taphonomic characteristics of assemblages as well as the stratigraphic context of fossiliferous units is required to evaluate spatial fidelity. Furthermore, uniformitarianism is assumed when applying most of these criteria to the fossil record. Nevertheless, a rigorous approach using multiple lines of evidence will generally allow for robust inferences concerning spatial fidelity.

Spatial fidelity: taxonomic and environmental patterns

The composition and structure of bioclasts, as well as the mode of life of the bioclast producer, affect transportability. Transport potential and spatial fidelity therefore vary among taxonomic groups, and for plants and animals with multielement skeletons, among the various bioclasts produced by an individual. In addition, spatial fidelity is dependent on depositional setting because physical and biological processes that cause transport change as the environment changes.

For most benthic marine invertebrates and micro-

fauna (particularly benthic foraminifera), out-of-habitat transport is rare in most settings ranging from intertidal flats to continental shelves. Based on live/dead comparisons, exotic bioclasts are typically minor components of most assemblages and are often derived from nearby habitats (Kidwell and Flessa 1995). Movement within habitats appears to be pervasive. Where documented in intertidal and shallow subtidal waters, however, resolution is of the order of tens of metres (Kidwell and Flessa 1995). Even in areas affected by episodic high-energy storms, transport of macrofauna is limited (Miller *et al.* 1992; Anderson *et al.* 1997). However, long-distance bulk-sediment transport (500 km), which displaces death assemblages *en masse*, can take place if a significant depositional gradient exists (see Kidwell and Flessa 1995).

At present, it is unclear whether large and small bioclasts (e.g. molluscs vs. benthic foraminifera) show significant differences in spatial fidelity. For example, differential transport of certain benthic foraminifera was inferred in one study from contradictory palaeoenvironmental interpretations based on molluscs vs. these foraminifera (Anderson *et al.* 1997). Alternatively, in another study no differential transport of molluscs or benthic foraminifera was inferred based on the congruence of spatial distribution patterns between the two groups (Warme *et al.* 1976). Presence or absence of differential transport, however, may relate to environmental setting. In the cases outlined, the former study was located on a high-energy continental shelf, whereas the latter was conducted in a protected back-reef lagoon.

Mode of life has a strong effect on transport potential and spatial fidelity of marine organisms. At one extreme, cementing encrusters and borers will tend to show high spatial fidelity. However, if these hard-substrate dwellers shed hard parts, those remains will tend to accumulate in adjacent habitats (Kidwell and Flessa 1995). Encrusting and boring communities may also lose their environmental context if the substrate they inhabit is transportable, although evidence such as geopetal structures can be used to detect such movement. At the other extreme, postmortem transport of 1000 km has been reported for shells of pelagic organisms such as *Nautilus*, although both modern and palaeontological evidence indicates that most external shells of cephalopods are deposited within their geographical range (Boston and Mapes 1991).

Death assemblages of terrestrial vertebrates typically show high fidelity to the living communities from which they are derived (Kidwell and Flessa 1995). In many settings, bones apparently reflect where an animal died even if that location may not be a 'characteristic' habitat for the animal, and spatial fidelity of species with limited geographical ranges is better than that for more wide-ranging animals (Behrensmeyer and Dechant Boaz 1980). Transport is more common in fluvial channel lags, although transport distances may be relatively short (<1000 m; Aslan and Behrensmeyer 1996). For both terrestrial and marine vertebrates, long-distance transport of floating carcasses occurs but is relatively rare (Kidwell and Flessa 1995). Spatial resolution of freshwater and terrestrial invertebrates is less well studied, although existing data suggest high spatial fidelity (Behrensmeyer and Hook 1992; Kidwell and Flessa 1995).

Plants produce a variety of bioclasts, from trunks to leaves to pollen, that differ greatly in transport potential and spatial resolution. However, environment of deposition plays a critical role in spatial resolution of floral material. Actualistic studies show that forest-floor leaf litter has high spatial resolution; macrofloral remains are generally dispersed no further than the height of the tree producing the litter (Kidwell and Flessa 1995). In general, bogs and swamps accumulate indigenous macrofloral assemblages, river and lake deposits can contain transported assemblages that none the less reflect local vegetation, and coastal and deltaic sediments may incorporate a largely allochthonous macroflora (Behrensmeyer and Hook 1992). Pollen assemblages generally have lower spatial resolution than macroflora, and often reflect regional rather than local distribution patterns (Behrensmeyer and Hook 1992). As with macroflora, spatial resolution varies greatly with the environment of deposition and is relatively high in soils, small lakes, bogs, and swamps (100 m resolution possible), but can be very low (entire drainage basin at best) for alluvial fan, fluvial, and marine deposits (Kidwell and Flessa 1995).

Other factors

Transport is not the only process that can affect the proportions of indigenous and exotic bioclasts in an assemblage. If the preservation potential of the indigenous assemblage is low, more durable exotic bioclasts may come to dominate the death assemblage (e.g. Martin and Wright 1988). Time-averaging (see Section 3.2.7), especially if encompassing a period of environmental change, can produce assemblages that appear to be spatially mixed. Indeed, time-averaging may be a much more common means of producing environmentally mixed assemblages than out-of-habitat transport (Kidwell and Flessa 1995). Teasing apart time-averaging and spatial mixing in fossil assemblages, however, may be very difficult because both leave similar taphonomic and sedimentary signatures in the rock record.

Conclusions and further directions

At first glance, the reliability of biotic remains as palaeoenvironmental indicators seems at odds with the

abundant evidence that bioclasts undergo some degree of postmortem transport and reworking. Actualistic studies, however, indicate that many death assemblages show high spatial fidelity to the local biota, although within-habitat transport appears to be pervasive. Bioclast composition and structure, the mode of life of the bioclast producer, and depositional processes all influence transport potential and spatial fidelity. In addition, criteria for distinguishing indigenous and exotic bioclasts and assemblages exist, and the expected spatial fidelity of a given assemblage in a given environment can be estimated. In fact, it may be possible to harness differences in transport potential to simultaneously compare local and regional biotas by differentiating transported and untransported bioclasts from the same samples.

References

Anderson, L.C., Sen Gupta, B.K., McBride, R.A. and Byrnes, M.R. (1997) Reduced seasonality of Holocene climate and pervasive mixing of Holocene marine section: Northeastern Gulf of Mexico shelf. *Geology* **25**, 127–130.

Aslan, A. and Behrensmeyer, A.K. (1996) Taphonomy and time resolution of bone assemblages in a contemporary fluvial system: The East Fork River, Wyoming. *Palaios* **11**, 411–421.

Behrensmeyer, A.K. and Dechant Boaz, D.E. (1980) The Recent bones of Amboseli Park, Kenya, in relation to East African paleoecology. In: A.K. Behrensmeyer and A.P. Hill, eds. *Fossils in the making*, pp. 72–92. University of Chicago Press, Chicago.

Behrensmeyer, A.K. and Hook, R.W. (1992) Paleoenvironmental contexts and taphonomic models in the terrestrial fossil record. In: A.K. Behrensmeyer, J.D. Damuth, W.A. DiMichele, R. Potts, H.-D. Sues and S.L. Wing, eds. *Terrestrial ecosystems through time: evolutionary paleoecology of terrestrial plants and animals*, pp. 15–136. University of Chicago Press, Chicago.

Boston, W.B. and Mapes, R.H. (1991) Ectocochleate cephalopod taphonomy. In: S.K. Donovan, ed. *The processes of fossilization*, pp. 220–240. Columbia University Press, New York.

Kidwell, S.M. and Flessa, K.W. (1995) The quality of the fossil record: populations, species, and communities. *Annual Review of Ecology and Systematics* **26**, 269–299.

Martin, R.E. and Wright, R.C. (1988) Information loss in the transition from life to death assemblages of foraminifera in back reef environments, Key Largo, Florida. *Journal of Paleontology* **62**, 399–410.

Miller, A.I., Llewellyn, G., Parsons, K.M. *et al.* (1992) Effect of Hurricane Hugo on molluscan skeletal distributions, Salt River Bay, St. Croix, U.S. Virgin Islands. *Geology* **20**, 23–26.

Warme, J.E., Ekdale, A.A., Ekdale, S.F. and Peterson, C.H. (1976) Raw material of the fossil record. In: R.W. Scott and R.R. West, eds. *Structure and classification of paleocommunities*, pp. 143–169. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania.

3.2.7 Time-averaging

K.W. FLESSA

Introduction

A time-averaged fossil assemblage is one in which the individuals preserved together were not alive at the same time. Time-averaging usually refers to accumulations of fossils that occurred over a nearly continuous time interval longer than the lifetime of a single individual rather than assemblages containing much older reworked fossils, even though these also contain fossils that were not alive at the same time. A condensed deposit, in which species from different biostratigraphic zones co-occur, lies at one end of the spectrum of time-averaging; the other extreme is defined by a community of living organisms buried and preserved in a single event.

Time-averaging is the process by which events that happened at different times appear to be synchronous in the geological record. In the case of fossil assemblages, this can occur when the rate of accumulation of fossil remains exceeds the rate of accumulation of sediments. Thus, sediment winnowing or low sedimentation rates can promote time-averaging if physical and biotic conditions permit the accumulation of skeletal remains. Nearly contemporaneous biogenic or physical reworking can also cause time-averaging. The remains of individuals that were not alive at the same time can be brought into proximity through the action of burrowing organisms or the erosion and winnowing of previously deposited skeletal material.

Time-averaging occurs because many fossil remains are quite durable. Although soft tissues rarely persist for long intervals, robust shells or teeth can withstand long intervals of abrasion or chemical solution. A newly dead mollusc shell can easily accumulate next to a long-dead and well-worn specimen, but it is unlikely that last year's flower will persist at the sediment surface long enough to be joined by this year's flower. The extent of time-averaging is a function of postmortem durability, sediment accumulation rate, and the rate of physical and biogenic reworking. Time-averaging varies in different sedimentary environments, and with different faunas and floras.

So-called analytical time-averaging (Behrensmeyer and Hook 1992) can occur as a consequence of the sampling or analysis of fossil assemblages. Pooling samples from different horizons, beds, or even formations will certainly result in a composite sample in which individual fossils were not contemporaneous. As with 'natural' time-averaging, the degree to which such temporal

mixing is a problem depends on the scientific question being addressed with the data from sampling.

Extent of time-averaging

Studies of time-averaging in Holocene and Late Pleistocene deposits can provide some estimates of the likely duration of time-averaging in other parts of the fossil record. Such young deposits often permit the direct dating of skeletal elements with techniques such as radiocarbon or amino-acid dating. Table 3.2.7.1 summarizes what is known about the extent of time-averaging, based on direct dating as well as estimates of time-averaging that rely on evidence from the sedimentary and biotic context of other fossil deposits.

Table 3.2.7.1 shows estimates of the typical amounts of time-averaging that can be expected among various biotas in various sedimentary environments. Particular fossil deposits may be time-averaged to greater or lesser degrees. In many cases, estimates of time-averaging are based on inferential methods or on only a few samples. Much remains to be done: no estimates of time-averaging are available for reef habitats, for example, and the estimate for planktic foraminiferans is based on a single study.

Nevertheless, some obvious generalizations can be made. First, deposits of very delicate biological materials are unlikely to be time-averaged: two flowers preserved on the same horizon are likely to be contemporaneous, while two shells in a coquina may be from individuals that died thousands of years apart. Second, many skeletal elements, such as bones, wood, teeth, and shells, can persist at or near the sediment surface for long periods of time. While this is not inevitable, it happens frequently enough to cause most fossil assemblages to be time-averaged over significant time intervals.

Table 3.2.7.1 Estimates of typical extents of time-averaging. (Derived from: Fürsich and Aberhan 1990; Kidwell and Bosence 1991; and Kidwell and Behrensmeyer 1993.)

Types of fossils	Typical scale of time-averaging (years)
Terrestrial environments	
Macroflora: fresh leaves and flowers	10^{-2}–10^{-1}
Macroflora: tree trunks	10^{1}–10^{3}
Macroflora: cuticle, leaf fall	10^{-1}–10^{0}
Macroflora: cones, seeds, bark	10^{0}–10^{1}
Pollen in lake laminae	10^{0}
Pollen in core tops	10^{1}
Vertebrates: surface accumulations	10^{1}–10^{3}
Vertebrates: cave deposits	10^{4}
Vertebrates: fluvial systems	10^{1}–10^{3}
Marine environments	
Macroinvertebrates: intertidal and nearshore	10^{1}–10^{3}
Macroinvertebrates: continental shelf	10^{3}–10^{4}
Benthic microfossils: terrigenous shelf	10^{-1}–10^{1}
Benthic microfossils: carbonate shelf	10^{1}–10^{4}
Planktic foraminiferans: oceanic	10^{1}–10^{3}

Controls on time-averaging

The best data on time-averaging come from studies of marine shelly faunas. More than 700 radiocarbon dates have been compiled on shelly material from Recent nearshore (<10 m depth) and shelf habitats (>10 m depth) (Flessa and Kowalewski 1994). The extent of time-averaging was measured by the maximum age of a shell in a surficial deposit, assuming that shells are still accumulating in that deposit. The median extent of time-averaging in nearshore deposits is approximately 1250 years, while that in shelf localities is approximately 9000 years (Fig. 3.2.7.1). The relatively limited extent of time-averaging in shelly nearshore deposits may be due to higher rates of shell destruction in shallower water. In addition, the continuing rise in sea level during the Holocene means that nearshore environments have been present where they are now for only the past few thousand years, thus limiting the potential extent of time-averaging.

The effect of sediment accumulation rate on time-averaging is evident in a comparison of intertidal and shallow subtidal molluscan assemblages in the Gulf of California (Meldahl *et al*. 1997). Time-averaging is significantly lower in coastal fan deltas than in sediment-starved intertidal flats. While all habitats display the typical right-skewed distribution of shell ages (Fig. 3.2.7.1a), shells tend to be younger in areas of high sedimentation rates than in habitats receiving little sediment input.

Assuming a continuous input of skeletal material through time, Fig. 3.2.7.2 illustrates how the interplay of shell destruction rate and sedimentation rate affects the degree of time-averaging. When both sedimentation rate and shell destruction rate are low, non-contemporaneous skeletal elements can accumulate; when both destruction and sedimentation rates are high, few shells will persist long after death, and those that do will be quickly buried and removed from the surface.

Biogenic and perhaps physical reworking must also play a major role in shallow marine habitats. Because shell destruction rates are high at the sediment–water interface, as a consequence of biological and physical processes, shells can only survive for long intervals of time if they are buried beneath the taphonomically active surface. Where ancient shells occur at the

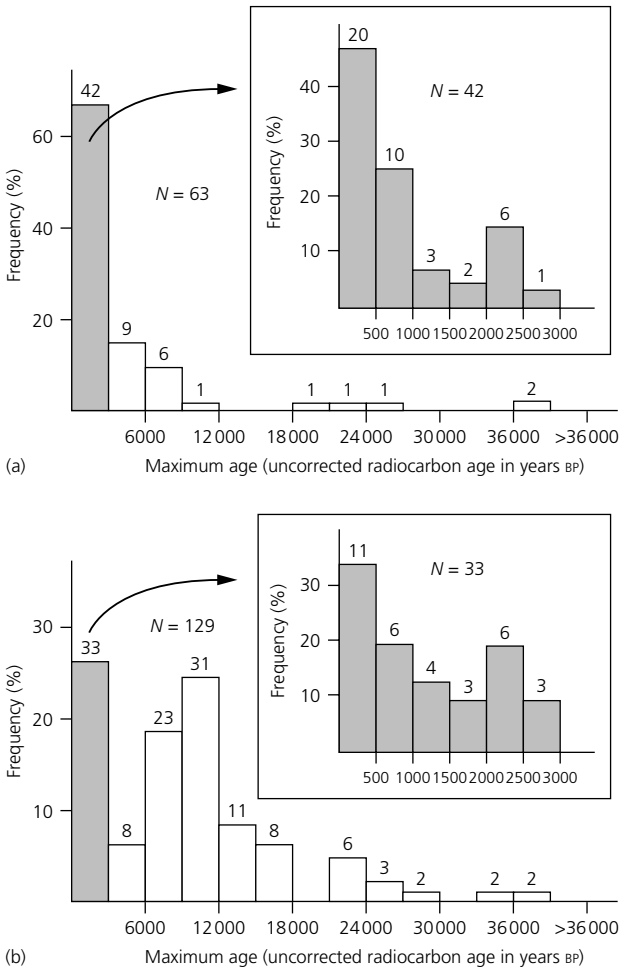

Fig. 3.2.7.1 Frequency distribution of maximum radiocarbon ages of shells. (a) Nearshore localities (median maximum age = 1250 years). (b) Shelf localities (median maximum age = 9190 years). Number above bar indicates absolute frequency in that age class; larger figures show frequency distributions using 3000-year age classes; inset histograms show frequency distributions in the 0–3000 years range with 500-year age classes. (From Flessa and Kowalewski 1994.)

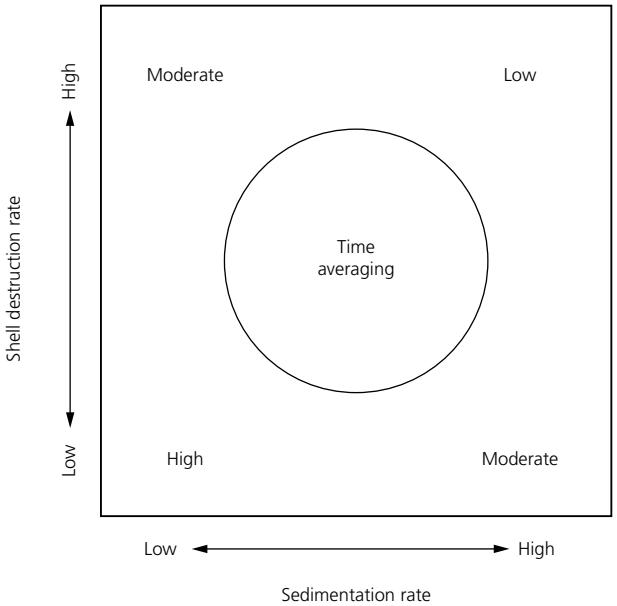

Fig. 3.2.7.2 Schematic diagram of how, under conditions of continuous shell input, the degree of time-averaging is regulated by the interplay of shell (or any potential fossil) destruction rate and sedimentation rate. Maximum time-averaging occurs when both destruction and sedimentation rates are low; minimum time-averaging occurs when both rates are high. (From Meldahl *et al.* 1997.)

sediment–water interface (e.g. the occurrence of 3000-year-old shells on the surface of tidal flats), this has been attributed to the burial and exhumation of shells by biogenic mixing and physical processes (Flessa *et al.* 1993).

Between-habitat transportation can also cause some degree of time-averaging. For example, coastal accumulations of the intertidal bivalve *Cerastoderma edule* in the southern North Sea contain individuals dating from 7000 BP—a time when sea level was lower and the coastline at least 10 km distant from its present location (Flessa 1998). In this instance, time-averaging resulted from the landward transport of shells during the Holocene transgression.

Effects of time-averaging

The accumulation of skeletal remains over some extended interval of time causes time-averaged fossil assemblages to differ from the original live communities in several ways (Fürsich 1978; Fürsich and Aberhan 1990). The fossil assemblage may include species that did not live at the same time as others because of variations in environmental conditions or irregular recruitment during the interval of time-averaging. As a result, the diversity and evenness of the fossil assemblage may exceed those of the living skeletonized fauna at any one time during accumulation. Patterns of relative abundance of species may also be altered. Species that are normally rare but experience brief increases in abundance may come to dominate the fossil assemblage if their skeletal remains resist postmortem destruction. Finally, the morphological variability within a time-averaged species population may exceed that present during any single living generation.

If time-averaging is caused entirely or in part by biogenic or physical reworking, then stratigraphic superposition may not be a good guide to relative age at very fine scales. Upward or downward mixing through burrowing or erosion and redeposition may cause hard parts from overlying or underlying beds to 'leak' into an accumulation. Under such circumstances, widely spaced

samples in a stratigraphic sequence may be necessary to ensure that none of the fossil specimens overlaps in age with specimens from overlying or underlying units. A sample separation of about 50 cm is necessary to avoid temporal mixing in deposits from extensively burrowed, sediment-starved tidal flats (Flessa *et al.* 1993).

However, time-averaging is not all bad news. Under many circumstances, a time-averaged accumulation could be a better representation of long-term environmental conditions than the biota present at one instant in time. The time-averaged biota may be a good sample of the natural range of environmental variation during the total interval in question, while a sample from one particular time may not be representative of typical conditions. Indeed, an accumulating death assemblage could be thought of as the result of the cumulative resampling of the living community of organisms with preservable parts. A time-averaged assemblage is more likely to contain rare and ephemeral species than any single sample of the source community.

The dating of many individuals from within shell beds suggests that at least some time-averaged assemblages do indeed reflect a time-weighted average of environmental conditions during the entire interval of time (Kowalewski *et al.* 1998). Furthermore, time-averaging may often be a continuous process that results in a complete record of faunal composition at a resolution of 50 years.

Recognizing time-averaging in the fossil record

Assemblages that are time-averaged are probably the rule rather than the exception in the fossil record. Even obrution deposits, in which rapid burial kills and then entombs a living community, are likely to contain the skeletal remains of organisms that died earlier and were simply lying about on the surface. The challenge therefore is to recognize degrees of time-averaging in fossil assemblages. Such an effort is important because any comparison of fossil communities must consider the extent to which they are similarly time-averaged. If the fossil communities have not been subject to similar degrees of time-averaging, differences in composition and structure could be consequences of differences in the degree of time-averaging.

Direct dating of fossil specimens can detect time-averaging. If radiocarbon or amino-acid dating reveals that specimens within a single deposit differ in their time since death, then the range or variance in age can be used as a measure of time-averaging. However, such direct dating of fossil remains is limited to Holocene and some Pleistocene deposits, and the expense of such techniques may preclude their routine application.

One or more indirect approaches to determining the extent of time-averaging are more commonly employed (see Fürsich and Aberhan 1990; Kidwell and Flessa 1995). Evidence on the extent of time-averaging in Recent sedimentary environments can sometimes be employed to infer its extent in similar ancient environments. This strictly actualistic approach may have its limitations inasmuch as ancient biotas may have differed in their taphonomic attributes, and some ancient sedimentary habitats may not be well represented today.

Sedimentary and geochemical evidence can also be employed to detect time-averaging. Low sedimentation rates may be reflected in the presence of erosional surfaces, well-developed soils, diagnostic minerals such as glauconite, or submarine hardgrounds. Extensively burrowed horizons in association with skeletal accumulations may indicate the temporal mixing of organic remains. If diagenetic alteration, vital effects, and transportation can be ruled out, and variation in isotopic or trace element composition between individuals exceeds that within a single individual, this may indicate that the individuals lived under different environmental conditions—presumably at different times.

Palaeoecological evidence may also indicate time-averaging. If the effects of transportation can be ruled out, the co-occurrence of ecologically dissimilar species could result from variation in environmental conditions through time at a particular site. For example, a mixture of brackish and fully marine species could result from temporally varying salinities. Similarly, the co-occurrence of infaunal species with encrusting species could suggest a change in substrate conditions during the interval of accumulation.

Under the right circumstances, taphonomic criteria can also be employed to detect time-averaging. If hard parts decay with increasing time since death, and if hard-part production is continuous, a mixture of states of preservation within a single species would suggest time-averaging. Such a 'taphonomic clock' seems to function over long time intervals because reworked fossils can often be recognized by their preservational state and adhering matrix. Although the variation in taphonomic condition increases with increasing time since death, well-preserved shells are not invariably the youngest ones in the assemblage (Flessa *et al.* 1993; Meldahl *et al.* 1997). Thus, over shorter time scales of decades to thousands of years, the taphonomic clock seems to be a poor time-keeper. Another approach is to consider the variation in preservation among species. The occurrence of only the most robust skeletal elements—teeth, for example—of one species, with the delicate articulated skeleton of another species is an indicator of some degree of time-averaging.

A classification of time-averaged assemblages

Fossil assemblages can be classified according to their degree of time-averaging (Kidwell and Bosence 1991). The categories are somewhat arbitrary, inasmuch as they divide up a continuous spectrum of time-averaging. Nevertheless, they are of value in providing guidelines for understanding the origin of fossil assemblages:

1 *Ecological snapshots* are fossil assemblages that accumulated with little or no time-averaging. Specimens are likely to be ecologically compatible, well preserved, articulated, and in place. The deposit itself may contain sedimentary evidence of rapid burial, and preservational state is likely to be relatively uniform within a species. Ecological snapshots probably provide temporal resolution at the scale of minutes to years. While probably rare, such deposits provide valuable glimpses of ancient communities sampled as an ecologist might sample a living community today.

2 *Within-habitat assemblages* record the accumulation of remains from a living community that persisted over a period of relative environmental stability. Although the species preserved are ecologically compatible, ephemeral species occur with persistent ones, many generations are represented, and preservational condition is likely to be variable within individual and among associated species. Geochemical environmental indicators are likely to vary within a narrow range. Such assemblages probably accumulated over time intervals ranging from years to thousands of years, and are probably common in the fossil record.

3 *Environmentally condensed assemblages* are formed over periods of significant environmental change. Such changes might include climate, substrate, sea-level rise, or elevation. Species present may be ecologically incompatible, though clearly untransported. Sedimentary evidence for low sedimentation rates may be present, and preservational condition may be variable within and among species. Geochemical environmental indicators may be highly variable among individuals and species. Environmentally condensed assemblages probably form over time spans ranging from hundreds to tens of thousands of years. Such assemblages are probably common in the fossil record.

4 *Biostratigraphically condensed assemblages* contain species with evolutionary ranges that do not overlap. One or more species became extinct or originated during the time of accumulation. Major environmental change has probably also occurred during accumulation, and sedimentary evidence for low sedimentation rates, winnowing, reworking, or omission surfaces is likely to be present. Preservational condition is likely to be generally poor, but highly variable. Such deposits are rare. They may represent time intervals from hundreds of thousands to millions of years.

References

Behrensmeyer, A.K. and Hook, R.W. (1992) Paleoenvironmental contexts and taphonomic models in the terrestrial fossil record. In: A.K. Behrensmeyer, J.D. Damuth, W.A. DiMichele, R. Potts, H.-D. Sues and S.L. Wing, eds. *Terrestrial ecosystems through time: evolutionary paleoecology of terrestrial plants and animals*, pp. 15–136. University of Chicago Press, Chicago.

Flessa, K.W. (1998) Well-traveled cockles: shell transport during the Holocene transgression of the southern North Sea. *Geology* **26**, 187–190.

Flessa, K.W. and Kowalewski, M. (1994) Shell survival and time-averaging in nearshore and shelf environments: estimates from the radiocarbon literature. *Lethaia* **27**, 153–165.

Flessa, K.W., Cutler, A.H. and Meldahl, K.H. (1993) Time and taphonomy: quantitative estimates of time-averaging and stratigraphic disorder in a shallow marine habitat. *Paleobiology* **19**, 266–286.

Fürsich, F.T. (1978) The influence of faunal condensation and mixing on the preservation of fossil benthic communities. *Lethaia* **11**, 243–250.

Fürsich, F.T. and Aberhan, M. (1990) Significance of time-averaging for paleocommunity analysis. *Lethaia* **23**, 143–152.

Kidwell, S.M. and Behrensmeyer, A.K., eds. (1993) *Taphonomic approaches to time resolution in fossil assemblages*. Short Courses in Paleontology, no. 6. The Paleontological Society, Knoxville, Tennessee.

Kidwell, S.M. and Bosence, D.W.J. (1991) Taphonomy and time-averaging of marine shelly faunas. In: P.A. Allison and D.E.G. Briggs, eds. *Taphonomy: releasing the data locked in the fossil record*, pp. 115–209. Plenum Press, New York.

Kidwell, S.M. and Flessa, K.W. (1995) The quality of the fossil record: populations, species, and communities. *Annual Review of Ecology and Systematics* **26**, 269–299.

Kowalewski, M., Goodfriend, G.A. and Flessa, K.W. (1998) High-resolution estimates of temporal mixing within shell beds: the evils and virtues of time-averaging. *Paleobiology* **24**, 287–304.

Meldahl, K.H., Flessa, K.W. and Cutler, A.H. (1997) Time-averaging and postmortem skeletal survival in benthic fossil assemblages: quantitative comparisons among Holocene environments. *Paleobiology* **23**, 207–229.

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3.3 Preservation in Different Ecological Settings

3.3.1 Major Biases in the Fossil Record

S.M. KIDWELL

Introduction

Palaeontologists investigate many different kinds of biological phenomena, ranging from the biomechanics of skeletal elements to the timing of mass extinctions, and so are concerned with the potential for taphonomic bias at many different scales (Table 3.3.1.1). The anatomical completeness of fossil preservation is of particular concern in studies of systematics and functional morphology; spatial fidelity (see Section 3.2.6), time-averaging (see Section 3.2.7), and ecological fidelity of fossil assemblages become significant in high-resolution evolutionary studies, palaeoecology, and biogeography; and the quality of time-series data and stratigraphic biases become especially significant in biostratigraphy, phylogeny, macroevolution, and evolutionary palaeoecology. Biochemical fidelity in investigations of isotopic and molecular palaeontology (e.g. studies of fossil diet, climate, DNA, biomarkers) could be added at the fine end of this spectrum. Any given fossil record (i.e. set of specimens, series of assemblages) thus has many different taphonomic qualities, of which only a subset may be relevant to the palaeobiological question at hand.

Although the quantification of bias is still very much at the frontier, both actualistic and stratigraphic studies indicate that most types of bias are the products of multiple intrinsic and extrinsic factors, whose rates and selectivities of damage are increasingly well known. Major sources of bias include: (1) the differing durabilities of biological materials (is the organism composed exclusively of highly volatile organic compounds or does it contain refractory organics and biominerals?); (2) the environment of accumulation (including the community of organisms that modify or destroy tissues after death, as well as the biogeochemistry of porewaters and the short-term dynamics of burial/exhumation); and (3) the postdepositional history of entombing sediments, which determines the ultimate fabric of the stratigraphic record. The challenge is to move from an appreciation of damage (i.e. states of fossil preservation, their origins, and the relative degrees of postmortem modification that they signify) to a quantitative assessment of bias (loss and other significant skewing of biological information). Biases clearly vary widely among major taxonomic groups, and probably across climatic/latitudinal and tectonic settings. The qualities of the fossil record may also have changed over geological time, a consequence of biological evolution (in both potential fossils and in tissue-destroying organisms), geological evolution of the Earth's surface (chemical changes in oceans and atmosphere, sea-level and climatic effects of plate tectonics, including latitudinal drift), and the cumulative effects of age (volume of available rock, cycles of diagenesis and tectonism).

Table 3.3.1.1 Qualities of the fossil record and sources of bias. (Adapted from Kidwell and Brenchley 1996.)

Aspect of quality	Sources of bias
Biochemical fidelity	Destruction, overprinting, and shifting of chemical compositions by diagenesis and metamorphism
Anatomical completeness	Destruction or incomplete mineral replacement of soft tissues; disarticulation, fragmentation, recrystallization, and deformation of mineralized skeletons
Spatial fidelity	Transport out of life position, life habitat, or biogeographical province
Temporal resolution	Mixing (time-averaging) of non-contemporaneous remains within the sedimentary column via physical or biological processes
Ecological fidelity	Selective destruction of species, morphs, and age classes, affecting presence–absence and relative abundance in fossil assemblages; bias from exotics and non-contemporaneous remains
Completeness of time series	Erosion or non-deposition of sediments, and taphonomic or diagenetic obliteration of fossils in surviving facies, creating gaps in the record
Stratigraphic bias	Non-random patterns both in the composition of facies because of cycles and secular trends in Earth's palaeogeography, and in the preservation of facies because their records are thin, localized, or readily eroded, preventing uniform sampling

Biases linked to inherent differences in biological materials

Perhaps the greatest bias in the fossil record is the divide between the poor to non-existent fossil record for organisms lacking mineralized or otherwise refractory skeletons, and the good to excellent record of organisms having such hard parts. Among living intertidal macrobenthos in Washington State, USA, for example, 100% of species with sturdy calcareous shells are from genera known to have a fossil record (shelled molluscs, barnacles, tube-secreting polychaetes, irregular echinoids), 73% of species with fragile skeletons or small isolated hard parts have a fossil record (e.g. arthropods, regular echinoids, asteroids, ophiuroids, holothuroids, sponges, tunicates, some nudibranchs and polychaetes), but none of the species lacking megascopic hard parts have a record (most polychaetes, nemerteans, ascidians, hydroids, anemones, sipunculans, flatworms, jellyfish, some nudibranchs, constituting 30% of the total fauna; Schopf 1978). These figures are typical for shallow-marine macrobenthic communities (reviewed by Kidwell and Bosence 1991), and analogous effects are known or expected among other groups, for example between agglutinated and mineral-secreting foraminiferans, mineralized and non-mineralized bryozoans, soft and stony corals, woody and non-woody plants, heavily and lightly sclerotized insects (reviewed by Kidwell and Flessa 1996). Taxonomically identifiable remains of organisms lacking megascopic hard parts (Schopf's 1978 last category)—and the preservation of soft tissues in general—require unusual environmental conditions that are geologically quite rare (see Sections 3.2.1 and 3.4). Such preservation has many positive consequences—high anatomical completeness, high temporal resolution (usually an instantaneous snapshot), high ecological fidelity—but biochemical fidelity may be low (tissues are generally preserved as mineral replacements or films, not as unaltered organic compounds) and stratigraphic horizons with comparable preservation may be so widely spaced that time series are weak.

Basic differences in body composition, linked strongly with phylogeny, thus have direct and fundamental effects on the qualities of the fossil record. The magnitude of the effect on time-averaging (time interval over which a fossil assemblage accumulated; see Section 3.2.7) and species richness in assemblages, for example, can be considerable. Quantitative information remains sparse but absolute scales of time-averaging in oxygenated environments range from ecologically instantaneous ('gelatinous' organisms which will be fossilized only under catastrophic burial or exposure limited to just a few days; flowers and lightly mineralized arthropods having maximum durabilities of weeks to months in sedimentary mixing zones) to ecologically prolonged (durable hard parts of land vertebrates and marine molluscs which can survive thousands to tens of thousands of years of attritional accumulation; Fig. 3.3.1.1).

The reworking of biological remains inherent to time-averaging has disparate effects on ecological fidelity: time-averaging tends to increase the species richness of taphonomically durable groups above standing diversities (by a factor of two or three among molluscs), mixing species from different generations or even community states, but reduces the diversity of fragile groups relative to the source community (by 25% or more; Kidwell and Flessa 1996). Some interesting concordances in durability and time-averaging occur across major taxonomic divides, for example between molluscs and non-agglutinating benthic foraminiferans, notwithstanding great differences in body size and skeletal microstructure. However, 'disharmonious' time-averaging is probably common in many taxonomically diverse assemblages, even if only hard part-producing groups are considered. The organic-rich shells of lingulid brachiopods, for example, can survive only a few days or weeks of reworking in intertidal sediments, and yet co-occur with very durable mollusc shells representing centuries to thousands of years of accumulation (see references in Section 3.2.7).

Even among groups with relatively high preservation potential, a proportion of taxa will be unrecorded or severely under-represented; quantifying this bias remains an important direction of taphonomic research (reviewed by Kidwell and Flessa 1996). The major factors in differential preservation of mineralized taxa are: (1) mineral content (from a few per cent to ≈99% dry weight within mineralized body parts); (2) mineral composition (aragonitic and calcitic forms of calcium carbonate, silica, and various organo-mineral forms of calcium phosphate are most common, e.g. 82% of bivalve genera with shells composed entirely of aragonite have a fossil record vs. 94% of genera with shells composed at least in part of calcite; Harper *in* Donovan and Paul 1998); (3) microstructure (variation in mineral crystallite surface area, percentage of organic matrix in the shell); (4) hard part size, shape, and density (intraskeletal porosity and growth form affect postmortem persistence and transport of bones, corals, and crinoids; size has a strong effect on pollen transport; Greenstein *et al*. *in* Donovan and Paul 1998; see Section 3.3.3); (5) tightness of skeletal articulation (e.g. differences among sea urchin families in anatomical completeness and in time-series data; Greenstein 1993); (6) body size (species representation in vertebrate death assemblages and age-class representation in mollusc assemblages); and (7) life habit (e.g. effects of epifaunal vs. infaunal life habit on preservation in life position among marine benthos).

Species that are rare in live communities (sparse or

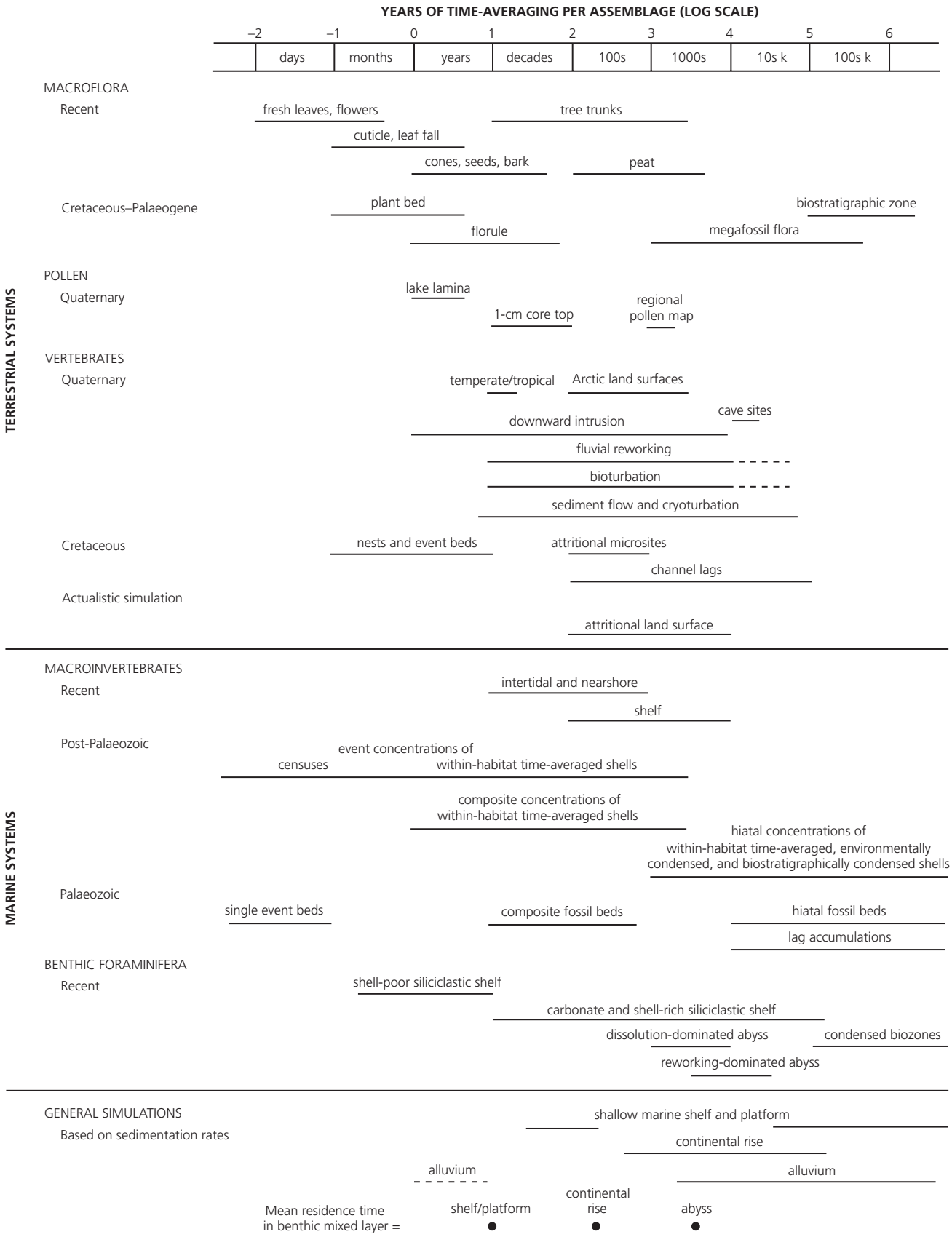

Fig. 3.3.1.1 Absolute durations of time-averaging. Estimates are based on diverse types of data, including extrapolations from modern rates of decay and disintegration, direct dating of specimens in modern death assemblages, inferred accumulation history of fossil concentrations, stratigraphic context, and probabilistic analysis of sedimentation rates. (Adapted from Kidwell and Behrensmeyer 1993.)

patchy distributions) also have low probabilities of being known from the fossil record. Because sampling is never complete, datasets are biased against rare species, so much so that some authors suggest ignoring them entirely (but see Culver and Buzas *in* Donovan and Paul 1998). However, relatively high ecological fidelity is indicated if species that are rare when alive are also rare in death and fossil assemblages. Living communities and local death assemblages show high statistical agreement in species rank-order for many groups (molluscs, land mammals, pollen, leaves; reviewed by Kidwell and Flessa 1996). Crabs and echinoids show poor live/dead agreements, and corals yield mixed results (good agreement between live communities and local Pleistocene fossil assemblages, but poor agreement between live and locally accumulating dead debris; Greenstein *et al*. *in* Donovan and Paul 1998).

Biases linked to postmortem environment

The major environmental divide in the quality of the fossil record is between land, which is dominated by erosion and weathering, and seas, which are overall sinks for sediment and are commonly oxygen-limited, especially in early diagenetic porewaters. Most palaeontologists would agree that land fossils are far less abundant and more patchy in distribution than marine fossils, even if microfossils are excluded (e.g. Benton and Simms 1995), but separating the effects of taphonomic environment from taxonomic composition is difficult. For example, is the fossil record of marine vertebrates (or arthropods or molluscs) more complete than the record of their terrestrial relatives? It probably is, but both realms are mosaics of physical and chemical conditions and, viewed globally, exhibit a comparable spectrum of fossil preservation, ranging from spectacular soft-tissue Lagerstätten to lags of only marginally identifiable skeletal debris. Consequently, differences in taphonomic bias across this environmental divide are probably more in degree than in kind.

A wide array of environmental agents and circumstances, acting alone or in combination, determine preservation in the very early phases of fossilization, and actualistic information on these factors drive expectations of bias in the fossil record. *Biological factors* in tissue preservation include the activities of predators and scavengers (which may destroy mineralized hard parts and/or transport remains out of the life habitat), bioturbators (which aerate and acidify porewaters, and also advect tissues), bioeroders/macerators, and encrusters (including microbial precipitation of minerals). *Physical factors* include timing of burial after death, sediment winnowing and physical reworking of specimens with or without out-of-habitat transport (see Section 3.2.6), net sediment accumulation rates (affecting average transit time to permanent burial level), light (UV weathering of bones; activity of photosynthetic bioeroders/encrusters), seasonality (pulsed vs. continuous carcass production), and specialized physical conditions of soft-tissue conservation (ice, desiccation). *Chemical factors* include oxygen levels (which drive hydrolysis and aerobic decomposers; anoxia excludes metazoan predators, scavengers, and bioturbators), mineral saturation state of water, acidity (antibacterial), sediment composition (availability of organic matter, iron and other metals for anaerobic decomposition pathways, silica for silicification, clays for organic adsorption), and nutrient levels (affecting organic production rates, intensities of bioerosion/encrustation; see Sections 3.2.2 and 4.2.8).

Most information on environmental trends in bias comes from studies in temperate latitudes. Marine basins show no simple monotonic trends in anatomical completeness and time-averaging with water depth or distance offshore (Fig. 3.3.1.2) because of the geomorphic complexity of coastal regions and the opposing trends of water energy (generally higher onshore) and net sediment accumulation rates (generally decreasing offshore in both siliciclastic and carbonate systems, but with onshore areas of erosion, bypass, and exposure). High-fidelity snapshot-type preservation is most common in lagoons and in offshore transition zones of maximum poststorm deposition. Relatively low-resolution environmentally condensed assemblages are most common in nearshore areas where facies shift rapidly, and net rates of sediment accumulation can be locally low. The ecological and spatial fidelity of molluscan death assemblages to local live communities is comparably high in level-bottom environments. These qualities of death assemblages do not appear to vary dramatically among freshwater, intertidal, coastal subtidal, and open shelf settings in temperate latitudes (reviewed by Kidwell and Flessa 1996), but the extent of latitudinal variation is still unknown.

In non-marine deposits, scales of time-averaging also vary dramatically among subenvironments (reviewed by Kidwell and Flessa 1996). Lakes provide both 'snapshot' censuses and time-averaged assemblages with decadal resolution (pollen, fish, insects, leaves, including some of the highest anatomical resolution of soft tissues); channel-fills and floodplain ponds typically yield time-averaged assemblages reflecting years to hundreds of years of skeletal accumulation; and most channel lags and palaeosols permit only hundreds to thousands of years' time resolution (Fig. 3.3.1.1). Spatial and ecological fidelity (presence–absence and rank order of species) are high for land mammals in the few environments tested, although differences in relative abundances in the living community are magnified in death assemblages. Spatial fidelity is high for pollen in all environments if only small-area lakes and other traps are sampled, and ecological fidelity is high if only wind-

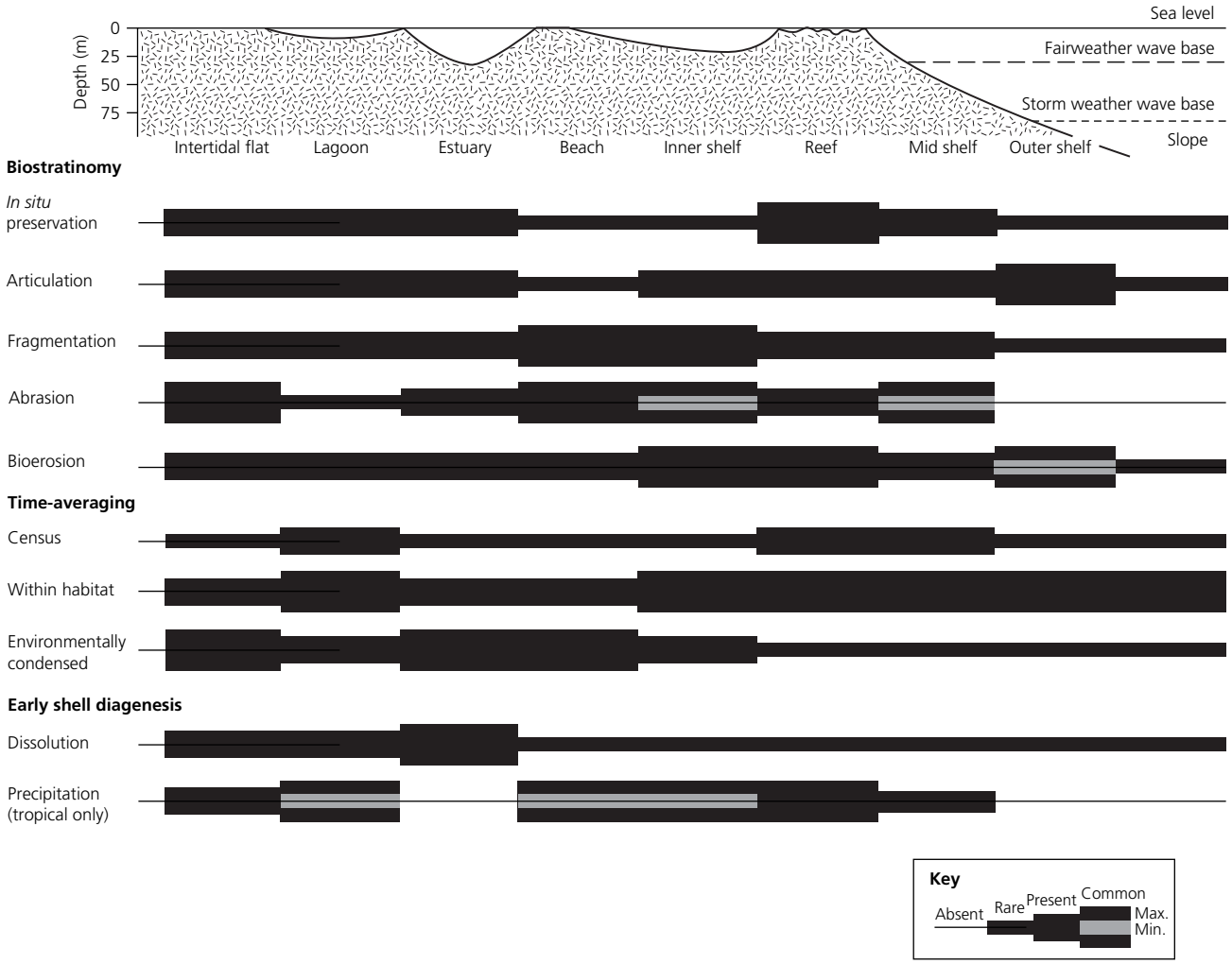

Fig. 3.3.1.2 Summary trends in types of damage and in bias for molluscan hard parts in marine environments. *In situ* preservation (in life position) and articulation signify high anatomical completeness. For absolute durations of time-averaging levels, see Fig. 3.3.1.1. (From Kidwell and Bosence 1991.)

pollinated plants are considered. Both qualities are high for leaf litter on temperate forest floors, but ecological fidelity is low for litter in tropical forests owing to their greater heterogeneity. Data on possible climatic trends in bias are sparse for other groups, but there appears to be lower spatial resolution in high-latitude insect assemblages than in low latitudes (Ponel and Richoux 1998), and greater durability and thus more time-averaging of land mammal bones in the Arctic than in temperate and tropical settings (Graham *in* Kidwell and Behrensmeyer 1993).

The potential biases imposed by environmental gradients can be avoided or minimized if care is taken to include only 'isotaphonomic' assemblages, i.e. fossil assemblages having taphonomically comparable histories of accumulation as judged from the state of preservation of surviving material and the sedimentological context.

Biases linked to sedimentary history and basin type

The ultimate filter on the quality of a particular fossil record is the fate of entombing sediments: diagenesis and erosion that locally degrade or obliterate the fossil record will limit both palaeogeographical (time-slice) and time-series information. Such destruction is not randomly distributed, but tends to be focused on the records of particular environments, sea-level phases, and tectonic settings/conditions. Palaeontologists have begun to evaluate the taphonomic consequences of this in a sequence-stratigraphic context at both basinal and global scales (Brett 1995; see Section 5.4.5). Within marine siliciclastic sequences, for example, transgressive tracts are commonly thinner and have greater potential for skeletal lags and environmental condensation of faunas; assemblages from regressive/progradational

phases tend to have higher time resolution and simpler histories of accumulation but are more likely to be affected by meteoric diagenesis and erosional removal; and sequence-bounding unconformities and other hiatuses are less severe and more localized in rapidly subsiding tectonic basins, so that time-averaging and taphonomic complexity of skeletal concentrations are lower than in other settings (Kidwell *in* Kidwell and Behrensmeyer 1993). Analogous stratigraphic bias is observed in non-marine vertebrate records. For example, low subsidence rates that favour prolonged fluvial reworking and close-stacking of channels reduce the preservation potential of snapshot assemblages, as observed both through base-level cycles and across foreland basin gradients in stratigraphic accommodation (e.g. Rogers *in* Kidwell and Behrensmeyer 1993 and references therein).

Hiatuses and extreme slow-downs in sedimentation, and diagenetic removal of fossils, make species ranges shorter and more discontinuous, a phenomenon evident at both sequence and larger scales (e.g. Paul and Donovan *in* Donovan and Paul 1998). In some instances, gradual trends may be made to appear sudden (e.g. erosional truncation causing last appearances to coincide at a single stratigraphic horizon), whereas in other instances coincidental events may be smeared into a gradual pattern (e.g. progressive change in facies, causing some species to disappear prematurely from a local record for ecological or taphonomic reasons). Because increased sampling cannot always compensate for such gaps, various methods have been developed to estimate the magnitude of the effect. These include the calculation of confidence limits for range end-points (based on gaps between occurrences within the known range, either biostratigraphic or biogeographical; Marshall *in* Donovan and Paul 1998), taphonomic control taxa (absence of a taxon is not a preservational artefact if another taxon with similar ecology and preservation potential is present, e.g. cyclostome bryozoans as control taxa for cheilostomes; Bottjer and Jablonski 1988), and 'Lazarus taxa' (the percentage of taxa that appear to become extinct, but then reappear later in the stratigraphic record, gives a measure of quality of time-series data for that interval; Jablonski 1986; see Sections 5.4.3 and 5.4.5).

There are also non-random patterns in the creation of environmental conditions favourable to fossilization, so that upland ponds/lakes, estuaries (flooding incised river valleys to make excellent vertebrate traps), anoxic lagoons (e.g. many Jurassic soft-tissue Lagerstätten), and authigenic phosphate and glauconite beds are most common during transgression. The high abundances of marine soft-tissue Lagerstätten during the Cambrian and Jurassic (Allison and Briggs 1993a), which are both transgressive phases of first-order sea-level cycles, perhaps reflect such geological control. Such geological factors create a fundamental fabric of facies types and gaps in the stratigraphic record, within which palaeontological collecting and analysis are constrained.

Megabiases—secular trends in qualities of the fossil record

There are many reasons to suspect that the quality of the fossil record may vary significantly with altitude/latitude/climate and over evolutionary time, due to differences in organisms and in geological conditions, but there are few empirical data relevant to these issues. This is of particular concern because of strong collecting bias by palaeontologists toward North America and Europe: both continents have drifted extensively through the Phanerozoic, so that their shallow seas were largely tropical during the Palaeozoic and non-tropical in later times. Collection bias has thus perhaps underestimated species richness per myr of the Permian by more than 100%, making it the most diverse period of the Palaeozoic, and underestimated post-Palaeozoic species richnesses by ≈50%, assuming that past latitudinal diversity gradients were as steep as in the Recent (Allison and Briggs 1993b). Other sampling factors with potential to bias large-scale palaeobiological patterns such as Phanerozoic diversity trends include the decline in outcrop area or rock volume with increasing geological age, and differences in monograph effort among geological periods and taxonomic groups (e.g. Sepkoski *et al.* 1981).

Geological factors are extremely important in patterning the record on time scales up to ≈50 myr (second-order stratigraphic sequences; see above). Longer-scale trends, however, appear to be driven primarily by changes in ocean/atmospheric chemistry and by evolution in biological processes, including both the production and the destruction/recycling of organic compounds and biominerals. Some of the most striking changes in styles of soft-tissue preservation occur in the late Precambrian–Cambrian interval. The advent of metazoan scavenging of collagen, the intensification of bioturbation, and physicochemical oceanographic changes in clay minerals have been variously invoked to explain the abrupt termination of the Ediacaran faunal record (sandstone impressions) and the exclusively Late Riphean to Middle Cambrian window of Burgess Shale-type preservation, in which non-mineralizing taxa are known from carbonaceous compressions (Jensen *et al.* 1998; Orr *et al.* 1998). In the Phanerozoic, changes in skeletal microstructure and ocean chemistry have been invoked to explain cyclic and secular changes in the quality of the marine microfossil record (Martin 1995). A proportional shift from calcite to aragonite precipitation among macrobenthos and a decline and retreat offshore of siliceous sponges may be responsible for a secular

decline in silicified shallow marine faunas, with implications for quality of skeletal preservation, intensity of palaeontological study, and numbers of Lazarus taxa (Schubert *et al*. 1997). An increase in the maximum thickness of dense-packed skeletal concentrations of benthic macrobenthos from the early Palaeozoic to the Neogene has been interpreted in terms of an increase in shell durability, the invasion by shell-producers of high-energy environments where postmortem winnowing is more common, and, perhaps, an increase in rates of shell production (Kidwell and Brenchley 1996). Evolutionary changes among shell-destroyers and purely geological factors evidently played a lesser role. The most likely effect on bias is an increase in time-averaging per assemblage over time and, perhaps in hand with this, a reduction in ecological fidelity: hand samples will capture different amounts of time depending on their geological ages. Taphonomic qualities of other records may also have changed in response to evolution of hard part producers, for example the land vertebrate record (e.g. dry land was not fully exploited until the late Palaeozoic, and mammal bones are generally more porous than reptile bones). However, net effects and specific drivers are difficult to predict given the many conflicting factors (e.g. changes in styles and metabolic rates of bone-crushing predators, no clear body size trends in prey, strong period-to-period bias in range of continental latitudes and aridity), and thus the determination of secular trends will almost certainly require an empirical survey of the fossil record itself.

References

Allison, P.A. and Briggs, D.E.G. (1993a) Exceptional fossil record: distribution of soft-tissue preservation through the Phanerozoic. *Geology* **21**, 527–530.

Allison, P.A. and Briggs, D.E.G. (1993b) Paleolatitudinal sampling bias, Phanerozoic species diversity, and the end-Permian extinction. *Geology* **21**, 65–68.

Benton, M.J. and Simms, M.J. (1995) Testing the marine and continental fossil records. *Geology* **23**, 601–604.

Bottjer, D.J. and Jablonski, D. (1988) Paleoenvironmental patterns in the evolution of post-Paleozoic benthic marine invertebrates. *Palaios* **3**, 540–560.

Brett, C.E. (1995) Sequence stratigraphy, biostratigraphy, and taphonomy in shallow marine environments. *Palaios* **10**, 597–616.

Donovan, S.K. and Paul, C.R.C., eds. (1998) *The adequacy of the fossil record*. John Wiley and Sons, Chichester.

Greenstein, B.J. (1993) Is the fossil record of regular echinoids really so poor? A comparison of living and subfossil assemblages. *Palaios* **8**, 587–601.

Jablonski, D. (1986) The evolutionary consequences of mass extinctions. In: D.K. Elliott, ed. *Dynamics of extinction*, pp. 183–229. John Wiley and Sons, New York.

Jensen, S., Gehling, J.G. and Droser, M.L. (1998) Ediacara-type fossils in Cambrian sediments. *Nature* **393**, 567–569.

Kidwell, S.M. and Behrensmeyer, A.K., eds. (1993) *Taphonomic approaches to time resolution in fossil assemblages*. Short Courses in Paleontology, no. 6. The Paleontological Society, Knoxville, Tennessee.

Kidwell, S.M. and Bosence, D.W.J. (1991) Taphonomy and time-averaging of marine shelly faunas. In: P.A. Allison and D.E.G. Briggs, eds. *Taphonomy: releasing the data locked in the fossil record*, pp. 115–209. Plenum Press, New York.

Kidwell, S.M. and Brenchley, P.J. (1996) Evolution of the fossil record: thickness trends in marine skeletal accumulations and their implications. In: D. Jablonski, D.H. Erwin and J.H. Lipps, eds. *Evolutionary paleobiology*, pp. 290–336. University of Chicago Press, Chicago.

Kidwell, S.M. and Flessa, K.W. (1996) The quality of the fossil record: populations, species, and communities. *Annual Review of Earth and Planetary Sciences* **24**, 433–464.

Martin, R.E. (1995) Cyclic and secular variation in microfossil biomineralization: clues to the biogeochemical evolution of Phanerozoic oceans. *Global and Planetary Change* **11**, 1–23.

Orr, P.J., Briggs, D.E.G. and Kearns, S.L. (1998) Cambrian Burgess Shale animals replicated in clay minerals. *Science* **281**, 1173–1175.

Ponel, P. and Richoux, P. (1998) Difficultés d'interprétation des assemblages de coléoptères fossiles quaternaires en milieu d'altitude. *Géobios, Mémoire Spécial* **21**, 213–219.

Schopf, T.J.M. (1978) Fossilization potential of an intertidal fauna: Friday Harbor, Washington. *Paleobiology* **4**, 261–270.

Schubert, J.K., Kidder, D.L. and Erwin, D.H. (1997) Silica-replaced fossils through the Phanerozoic. *Geology* **25**, 1031–1034.

Sepkoski, J.J. Jr, Bambach, R.K., Raup, D.M. and Valentine, J.W. (1981) Phanerozoic marine diversity and the fossil record. *Nature* **293**, 435–437.

3.3.2 Benthic Marine Communities

W.D. ALLMON

Introduction

In diversity of taxa and abundance of individuals, benthic marine invertebrates constitute the majority of the fossil record. Although it is likely that the fossil record of benthic marine organisms is among the most complete of all major environmental settings, not all benthic marine invertebrate species in a community are equally likely to be fossilized, and their relative abundances or ecological relationships may not be preserved. Analysis of the likelihood of preservation of particular taxa, and of benthic marine communities in general, has important implications for understanding patterns of evolution of individual organisms and communities, as well as larger patterns of diversity and

Table 3.3.2.1 Factors affecting preservation in benthic marine communities.

Characteristics of individual taxa
Presence of robust, mineralized skeletons
High abundance
Body size
Stability of population
Geographical range
Stratigraphic range
Characteristics of communities
Number of highly preservable taxa
Primary productivity
Characteristics of sedimentary environments
Sedimentation rate
Degree of time-averaging
Degree of chemical carbonate destruction (dissolution)
Degree of physical carbonate destruction (fragmentation, abrasion)
Degree of biological carbonate destruction (bioerosion)
Characteristics of geological history
Abundance of fossiliferous rock

extinction. Preservation in benthic marine communities has generally been analysed in three ways (Valentine 1989): (1) studies of the modern fauna ('actuopalaeontology'), to estimate actual and potential recruitment of organic remains into the record; (2) studies of the mode of formation, completeness, and accumulation span of individual fossil assemblages; and (3) quantitative studies of the completeness and temporal resolution of the biostratigraphic record. Actuopalaeontological studies of modern benthic communities offer a unique perspective on the fossil record and suggest that, within certain limits, preservation is relatively good.

Factors affecting preservation

A number of factors affect preservation of benthic individuals, taxa, and communities (Table 3.3.2.1). Within a given benthic marine community, highest preservation probability is shown by taxa with robust mineralized skeletons, which are abundant, large-bodied, and have stable populations. For the fossil record as a whole, benthic marine taxa with the highest preservation potential are those characterized by broad geographical distribution and long stratigraphic range. Among taxa with these characteristics, preservation potential appears to be controlled by relative abundance, the geological preservation of fossiliferous rock (Valentine 1989), and perhaps the frequency with which environments supporting large numbers of individuals occur. Across the range of benthic environments preservation

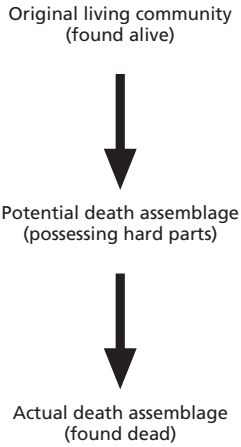

Fig. 3.3.2.1 Stepwise approach for considering the preservation potential of a living benthic marine community.

is highest where removal of a potential fossil from the taphonomically active zone is rapid. Time-averaging (see Section 3.2.7) may assist preservation of some kinds of information, while obscuring others (Kidwell and Flessa 1995). All other factors being equal, rare taxa should have lower preservation potential, but time-averaging increases the probability that rare species will be preserved, and greater sampling intensity increases the probability that they will be discovered (Valentine 1989).

Data from modern benthic communities

Examination of Recent benthic macroinvertebrate communities suggests a stepwise approach for considering their preservation potential and 'fidelity' (Fig. 3.3.2.1). Most benthic marine species lack mineralized skeletons; these 'soft-bodied taxa' degrade rapidly, and usually disappear shortly after death. The proportion of taxa in Recent benthic macroinvertebrate communities possessing resistant hard parts ('preservable taxa') range from 0 to 70% or more, with a mean value of about 30% (Table 3.3.2.2). There does not appear to be a clear correlation between proportion of skeletonized taxa and water depth or sediment grain size (Kidwell and Bosence 1991).

Within this 'preservable' fraction, the probability of taxonomic representation is relatively high. More than 75% of such species living in intertidal to mid-shelf depths are also recorded dead in the same habitat (Table 3.3.2.2). A smaller percentage of species found dead, however, are also found alive. This appears to be because most death assemblages are time-averaged whereas most live communities are sampled only once, providing an inadequate basis for comparison (Kidwell and Bosence 1991). Live communities subjected to longer sampling programmes show improved agreement

Table 3.3.2.2 Results of analysis of previous studies of Recent benthic marine communities and assemblages. (Data from Kidwell and Bosence 1991.)

	Range	Mean(s)
Potential death assemblage (i.e. % of species in live community with mineralized hard parts)	0–70	30
Actual death assemblage (i.e. % of species in live community found dead)	30–100	75–98
Dead taxa found alive (i.e. % of species in death assemblage found alive)	4–100	33–57
Dead individuals found alive (i.e. % of individuals in death assemblage from species found alive)	6–100	70–90

between lists of live and dead taxa. This suggests that many species found 'dead only' are not transported from other habitats, but have not yet been sampled live because of patchy or ephemeral populations (Kidwell and Bosence 1991). Similarly, the average percentage of dead individuals from species found alive in modern benthic marine assemblages is high (Table 3.3.2.2), suggesting that species not sampled alive are represented by few or no dead individuals.

The preservation potential of the relative numerical abundance of 'preservable' taxa is more complex than that of their taxonomic composition. Although the relative abundance of 'preservable' taxa may be only imperfectly represented in the preserved assemblage (Fig. 3.3.2.2), overall there may be a high degree of fidelity (Kidwell and Bosence 1991; Kidwell and Flessa 1995); most modern molluscan death assemblages, for example, agree closely with relative abundances of the living community. Differences lie in details that may be locally significant, specifically: (1) about half of the most abundant taxa in death assemblages are the most abundant taxa in the living community; (2) the most abundant live taxa generally account for slightly more than half of all individuals in the death assemblage; and (3) less than half of the most abundant dead taxa occur in the same order or ranked abundance as they do in the living community (these taxa account for about one-third of all individuals in the death assemblage) (Kidwell and Bosence 1991).

What we know vs. what we want to know

Species composition and diversity

Based on estimates that approximately 250 000 species have been described from the fossil record (mostly benthic marine invertebrates) (Raup and Stanley 1978), and depending on assumptions of (1) total present species diversity, (2) pattern of diversity change over the Phanerozoic, and (3) average species duration (turnover), estimates of the total taxonomic completeness of the Phanerozoic fossil record range from 1 to 14%. As a broad generality, however, approximately 30% of the species within a particular benthic marine community may be expected to leave a fossil record.

Abundance and biomass

Even communities that contain many biomineralized taxa are commonly dominated numerically by soft-bodied forms, thus yielding poor agreement between dominance-based diversity measures for the total living community and its shelly death assemblage (Kidwell and Bosence 1991). Within the skeletonized component, however, estimates of relative abundance may be reasonably reliable, depending on local factors and how the estimates are obtained. Biomineralized forms may dominate benthic communities in biomass because of their frequently larger body size, even when they do not dominate in numerical abundance (Kidwell and Bosence 1991). Among preservable taxa the original relative abundance may or may not be poorly preserved, but numerical abundance data may indicate real variation in the ecological success of species when compositions of both live and dead shells are examined over time scales of more than a few years (Powell *et al.* 1989; Kidwell and Bosence 1991). Furthermore, postmortem dissolution of hard parts appears to have a disproportional effect on the more ephemeral constituents of communities (i.e. short-lived small or opportunistic forms), so that the temporally persistent elements of the community are reflected in the skeletonized death assemblage (Kidwell and Bosence 1991).

Spatial distribution

Except for instances of extremely rapid burial, most fossil remains consist of disarticulated skeletal elements separated by some distance from other parts of the same skeleton, or of single-element skeletons transported some distance from the place of death (Kidwell and Flessa 1995). Actuopalaeontological studies, however, indicate that most postmortem movement of organic remains is within the geographical range of the original life habitat, or at least within the time-averaged range of the species. Significant out-of-habitat transport appears limited to instances that are recognizable by independent geological criteria (e.g. abrasion, fragmentation, encrustation; Powell *et al.* 1989), which should be examined carefully before a conclusion on transport (or lack of it) is made (Kidwell and Flessa 1995).

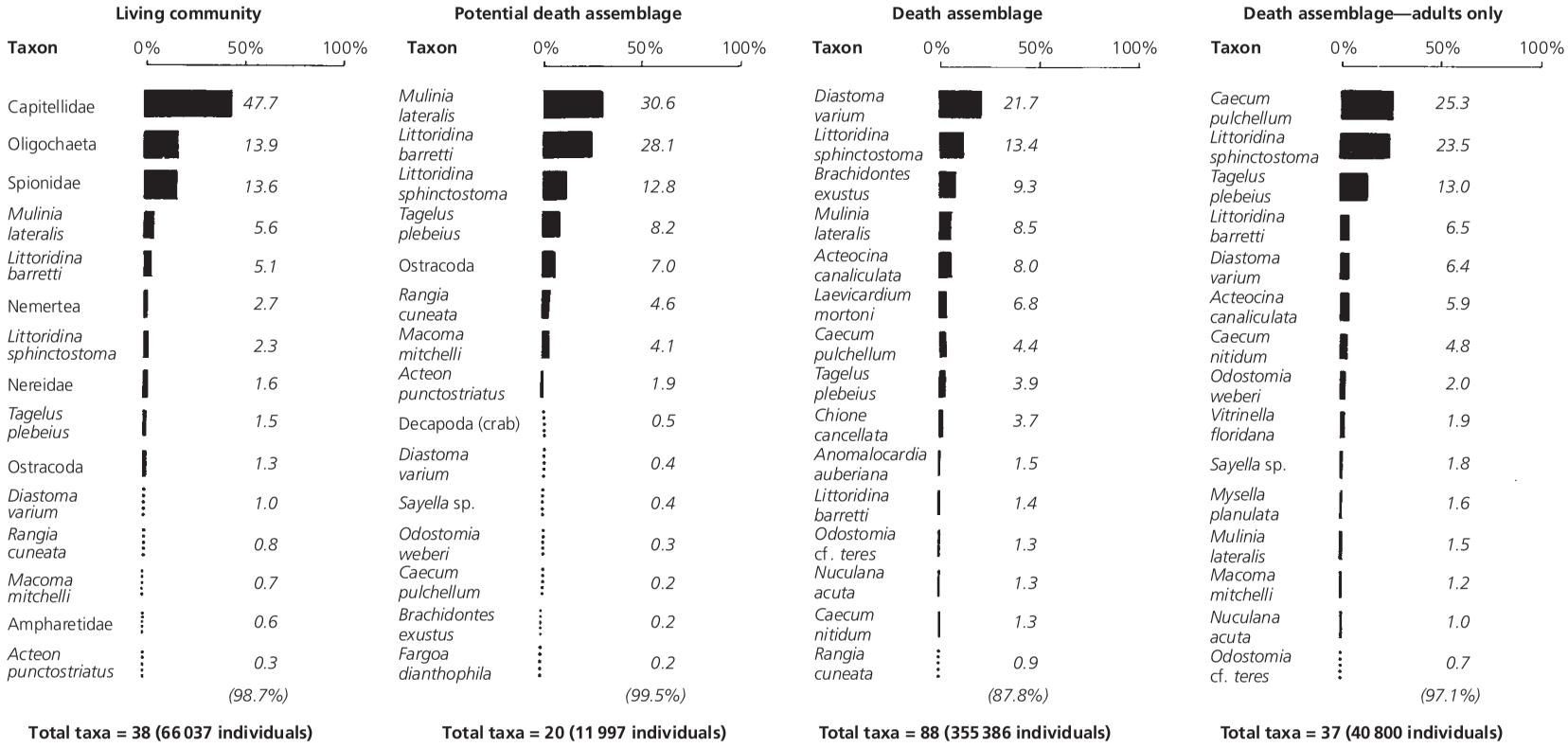

Fig. 3.3.2.2 Data for Recent benthic marine communities in Copano Bay, Texas. The 'potential death assemblage' includes those taxa with mineralized shells. The 'death assemblage' includes only those taxa actually collected dead. Note the changes in rank abundance of individual taxa, e.g. *Mulinia lateralis*. Dotted lines, <1%. (From Staff *et al.* 1986.)

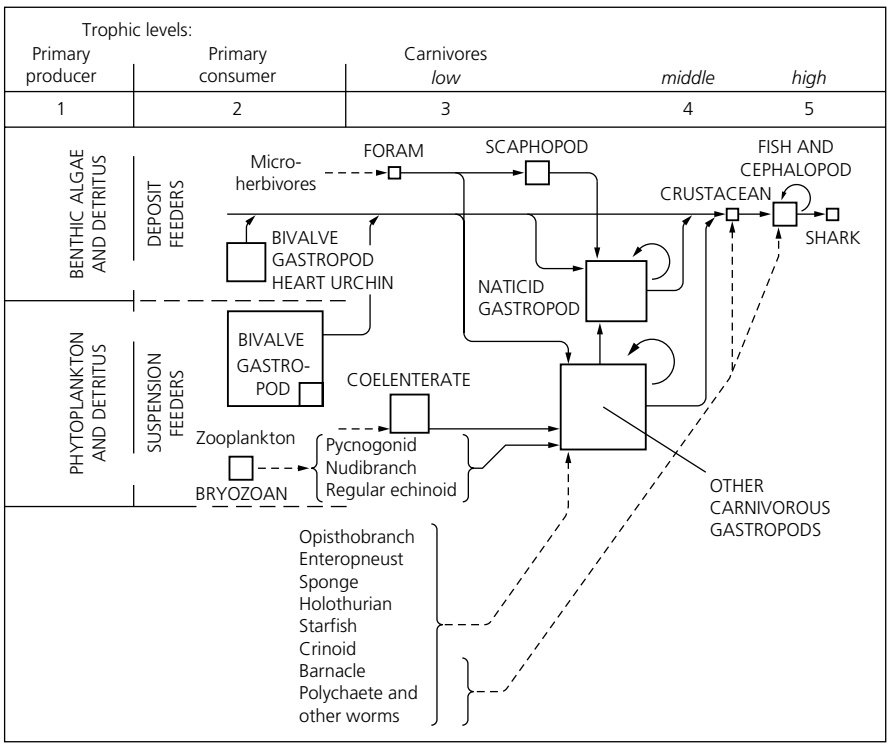

Fig. 3.3.2.3 Trophic web reconstruction for the benthic and pelagic community of the Stone City Formation, Middle Eocene, Texas. Box sizes are proportional to numbers of individuals at each position in the trophic web. Solid lines and capital lettering indicate components present in the fossil assemblage and feeding relationships documented in the fossil assemblage or based on comparison with modern analogues. Dashed lines and lower case lettering indicate inferred components and relationships in the original living community, based on comparison with modern communities involving taxa not preserved as fossils. (From Stanton and Nelson 1980.)

Trophic structure

Reconstructing trophic relations and other biotic interactions of ancient benthic marine communities depends both on what is preserved and what can be inferred reliably from comparison with modern communities. Use of biomass of preserved taxa for such reconstructions rather than numerical abundance minimizes the biases of time-averaging and non-preservation (Powell *et al.* 1989). Palaeontological trophic analyses most often address only the biomineralized portion of ancient communities. The reliability of these reconstructions reflects the usually high fidelity of records of these taxa. Attempts to reconstruct the guild and trophic structure of the total (preserved and unpreserved) community can be an informative exercise, as it forces critical, explicit, and quantitative examination of what is known and what is assumed (Fig. 3.3.2.3).

References

Kidwell, S.M. and Bosence, D.W.J. (1991) Taphonomy and time-averaging of marine shelly faunas. In: P.A. Allison and D.E.G. Briggs, eds. *Taphonomy: releasing the data locked in the fossil record*, pp. 116–211. Plenum Press, New York.

Kidwell, S.M. and Flessa, K.W. (1995) The quality of the fossil record: populations, species, and communities. *Annual Review of Ecology and Systematics* **26**, 269–300.

Powell, E.N., Staff, G.M., Davies, D.J. and Callender, W.R. (1989) Macrobenthic death assemblages in modern marine environments: formation, interpretation, and application. *CRC Critical Reviews in Aquatic Sciences* **1**, 555–589.

Raup, D.M. and Stanley, S.M. (1978) *Principles of paleontology*, 2nd edn. W.H. Freeman, San Francisco.

Staff, G.M., Stanton, R.J. Jr, Powell, E.N. and Cummins, H. (1986) Time averaging, taphonomy and their impact on paleocommunity reconstruction: death assemblages in Texas bays. *Bulletin of the Geological Society of America* **97**, 428–443.

Stanton, R.J. Jr and Nelson, P.C. (1980) Reconstruction of the trophic web in paleontology: community structure in the Stone City Formation (Middle Eocene, Texas). *Journal of Paleontology* **54**, 118–135.

Valentine, J.W. (1989) How good was the fossil record? Clues from the Californian Pleistocene. *Paleobiology* **15**, 83–94.

3.3.3 Ancient Reefs

J.M. PANDOLFI

Introduction

Reefs are one of the most ancient and diverse ecosystems on Earth. From Precambrian stromatolites to Australia's Great Barrier Reef, they have captured the imagination of generations of Earth and life scientists. Their porous lithology also provides a reservoir for many of the world's oil and gas deposits. Given this wealth of academic and economic interest, it is surprising how little is

known about the preservation of reefs and the amount and nature of information loss between once-living and fossil reef systems.

Reefs are biologically produced structures that stand in relief higher than the surrounding oceanic substrates, exerting some degree of control over oceanographic processes (Hubbard 1997). The sedimentary environment in which reefs grow is crucial to their final composition and structure (Scoffin 1992). Indeed, many so-called 'reef' deposits are not the product of an *in situ* interlocking framework of skeletons, but comprise loose assemblages of reef-building organisms 'floating' in a matrix of reef-derived debris (Hubbard 1997). The final fabric of the reef deposit depends on both constructional and destructional processes. Constructional aspects include carbonate production by both primary (e.g. stromatolites, corals, rudistids) and secondary (i.e. other reef inhabitants with hard skeletons, such as coralline algae) framework growth, patterns of sedimentation and burial (sediment trapping within the reef), and marine cementation. Destructional components include mechanical and biological erosion, sediment removal, and postburial diagenesis.

Critical factors affecting reef preservation

Most ancient reef species are extinct. Soft-bodied algal reefs are considered to stand much less chance of being preserved than the biomineralized skeletons of Cambrian archaeocyathids, Carboniferous fusulinids, Cretaceous rudistids, or Miocene corals. But how much more or less completely preserved are fossil assemblages from a Carboniferous Walsortian mound deposit than those from the Permian reefs of Texas? Are there any standards by which to judge the preservation of reefs during different geological periods, or are reefs problematic to study in this way due to their ever-changing taxonomic composition?

Only a minor proportion of the overwhelming diversity of life inhabiting reefs has biomineralized skeletons. Thus, only a small fraction of the organisms that once inhabited these ecosystems is represented in the rock record. The greatest information loss has been recorded for cryptic reef cave communities, approximating 85% of areal coverage, 62% of original richness, and 58% of original dominance diversity (Rasmussen and Brett 1985). How can we understand the fate of the non-fossilized component of the reef biota, much less infer anything about their ancient ecology?

Many reefs through geological time are produced biogenically, so 'the rates of biogenic production and sedimentary accumulation of the different types of skeletal remains…controls the concentration (or dilution) of the hard parts of any particular species' (Scoffin 1992, p. 57). This results in feedback between environmental and biotic processes on the living reef, with dramatic implications for the preservation of fossil reefs. For example, reefs may 'keep-up', 'catch-up', or 'give-up' when sea level rises (Neumann and Macintyre 1985). Keep-up reefs can preserve a large volume of organic remains in a very short amount of time, whereas give-up reefs may grow very little and face erosional processes when sea level drops or during a stillstand.

Finally, many reef inhabitants biologically degrade or destroy the reef, a process called bioerosion (see Section 3.2.2). In living reefs the principal bioeroders are grazers (echinoids, fish, gastropods, and chitons), etchers (bacteria, fungi, and algae), and borers (sponges, bivalve molluscs, and sipunculan and polychaete worms). Bioerosion can facilitate physical erosive processes. For example, dead corals that have been bored by clams suffer greater damage under high wave energy conditions, especially during storms, than those which have not been so infested. In addition, disturbance by storms may enhance biological degradation as new surfaces are exposed to colonization by bioeroding organisms.

Clues from the Quaternary

During the last decade, palaeoecological studies of Quaternary coral reef ecosystems have demonstrated that the fossil record preserves a wealth of information relevant to current investigations of both global change and environmental perturbations on a local scale. Thus taphonomic studies take on an additional objective: to assess the accuracy with which the recent history of ecosystems is preserved. These studies are particularly relevant to a variety of problems presently facing community ecologists and marine resource managers.

One of the most illuminating ways to assess Quaternary reef preservation is through comparative study of the transition from life to death assemblages within the zone of active degradation in the modern coral reef ecosystem (e.g. Pandolfi and Greenstein 1997). The ecological zonation (in species relative abundance, presence–absence, diversity, and growth form) commonly exhibited among reef coral life assemblages is reflected in their corresponding death assemblages. This correspondence occurs even though the life and death assemblages differ according to their species distribution patterns (Fig. 3.3.3.1). For example, massive coral growth forms tend to be under-represented and other coral growth forms to be over-represented in Floridian death assemblages relative to their original life assemblages. Death assemblages can also provide clues about the nature of reef communities in the not too distant past. For example, coral death assemblages from the North Atlantic and Caribbean Province reflect communities that were more typical of Caribbean reefs prior to the degradation of the 1980s and 1990s than of adjacent contemporary life assemblages (Greenstein *et al.* 1998a). These studies have also shown that different reef settings

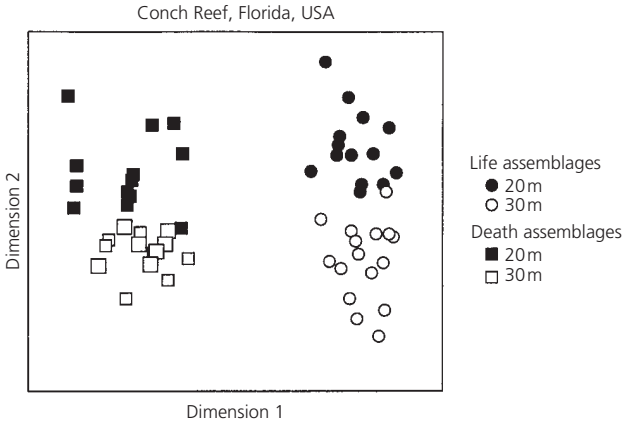

Fig. 3.3.3.1 Multidimensional scaling ordination of taxonomic composition in modern life and death coral assemblages from 20 m and 30 m water depths at Conch Reef in the Florida reef tract, USA. Note the displacement of the life assemblages from the death assemblages along the horizontal axis, suggesting differences in community composition between them. However, differences in the relative abundance of live reef coral assemblages between depths, shown along the vertical axis, are reproduced in the death assemblages. (From Pandolfi and Greenstein 1997.)

are preserved in different ways, so separate taphonomic studies must be made for each individual reef environment. When adjacent fossil assemblages are compared to their live and dead counterparts, they show high degrees of fidelity, illustrating that the fossil record of Quaternary coral reefs is extraordinary and can provide a very reliable tool with which to address a variety of ecological issues (Greenstein *et al*. 1998b).

Where do we go from here?

A modelling approach could provide useful information for understanding the relative influence of various sedimentological and taphonomic variables on the preservational potential of various reef settings through geological time. For example, how do such variables as the rate of carbonate production vs. bioerosion, the rate of carbonate transport into and out of the reef, and resistance of the primary framework builder to physical and biological degradation interact on reefs to produce the final fossil assemblage seen in the ancient record?

Empirical approaches such as those cited above should be extended to include extinct organisms. For example, what percentage of Cambrian archaeocyathid species available in the species pool actually comprise local reef assemblages? How do taxonomic dominance patterns relate to the robustness of the primary framework skeleton? Finally, very little is known about the taphonomic fate of most non-primary framework reef dwellers, even those with a hard skeleton. By examining the preservation dynamics of this portion of the reef community, we can begin to understand the way in which an enormous amount of biological diversity on reefs is incorporated into the fossil record. This information will dramatically increase our knowledge of reef biodiversity through time and its response to environmental change.

One of the ways in which palaeontologists can help to safeguard modern reefs for future generations is to understand the way in which reefs from all ages have responded to environmental crises. But this contribution can only be made by obtaining a thorough understanding of the taphonomy of reefs in geological time. Until we provide a protocol for understanding how reefs are preserved we will lack the tools needed to use the past as a key to the future. Perhaps this is presently the greatest challenge to the science of reef taphonomy.

References

Greenstein, B.J., Curran, H.A. and Pandolfi, J.M. (1998a) Shifting ecological baselines and the demise of *Acropora cervicornis* in the western North Atlantic and Caribbean Province: a Pleistocene perspective. *Coral Reefs* **17**, 249–261.

Greenstein, B.J., Pandolfi, J.M. and Curran, H.A. (1998b) The completeness of the Pleistocene fossil record: implications for stratigraphic adequacy. In: S.K. Donovan and C.R.C. Paul, eds. *The adequacy of the fossil record*, pp. 75–109. John Wiley, New York.

Hubbard, D.K. (1997) Reefs as dynamic systems. In: C. Birkeland, ed. *Life and death of coral reefs*, pp. 43–67. Chapman and Hall, New York.

Neumann, A.C. and Macintyre, I. (1985) Reef response to sea level rise: keep-up, catch-up or give-up. *Proceedings of the 5th International Coral Reef Congress, Tahiti* **3**, 105–110.

Pandolfi, J.M. and Greenstein, B.J. (1997) Preservation of community structure in death assemblages of deep water Caribbean reef corals. *Limnology and Oceanography* **42**, 1505–1516.

Rasmussen, K.A. and Brett, C.E. (1985) Taphonomy of Holocene cryptic biotas from St Croix, Virgin Islands: information loss and preservational biases. *Geology* **13**, 551–553.

Scoffin, T.P. (1992) Taphonomy of coral reefs: a review. *Coral Reefs* **11**, 57–77.

3.3.4 Marine Plankton

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Introduction

The taphonomic record of fossil marine plankton provides important clues to the evolution of the biogeochemical cycles of carbon, phosphorus, and silica. Although present in the Palaeozoic, siliceous and calcareous plankton did not become important links in bio-

geochemical cycles until the Mesozoic because of secular patterns of preservation and nutrient availability (see Martin 1996, 1998 for extensive references).

The Palaeozoic record of calcareous plankton

Metamorphic decarbonation of calcareous oozes in deep-sea trenches influences the biogeochemical carbon cycle on a geological time scale. Based on presence–absence data of the fossil record, calcareous nannoplankton (e.g. coccolithophorids), which form these oozes, did not evolve until the Late Triassic (Fig. 3.3.4.1a), and their role in the carbon cycle presumably began in earnest no earlier than about mid-Jurassic (≈150 Ma). Deposition of extensive cratonic limestones may have kept the calcite compensation depth (CCD) between ≈1–2 km during the early Palaeozoic, thereby preventing ooze formation (Boss and Wilkinson 1991); high atmospheric pCO_2 also enhanced dissolution of any coccoliths deposited in epeiric seas. Thus, virtually all Cambro-Devonian calcareous plankton dissolved, leaving behind mainly dissolution-resistant non-calcareous taxa (acritarchs, radiolaria, graptolites, conodonts). Enigmatic calcareous nannofossils have been reported from cratonic sediments of the Palaeozoic (Fig. 3.3.4.1a), but these occurrences have typically been dismissed either as contaminants from younger rocks or for lack of adequate description. Falling sea level during the Permo-Carboniferous (Fig. 3.3.4.1b) no doubt resulted in erosion of cratonic limestones, thereby causing the CCD to deepen sufficiently to intersect mid-ocean ridge crests by the late Pennsylvanian (≈300 Ma). This process, in turn, was instrumental in initiating the deposition of incipient calcareous oozes before their consistent preservation began in the Mesozoic.

Another factor in the preservation of calcareous oozes may have been nutrient availability. Total nutrient availability was presumably too low in the Cambro-Devonian to support high densities of phytoplankton. As dissolved nutrients became available, they were quickly sequestered into living (and eventually dead) biomass, thereby resulting in extremely low nutrient availability

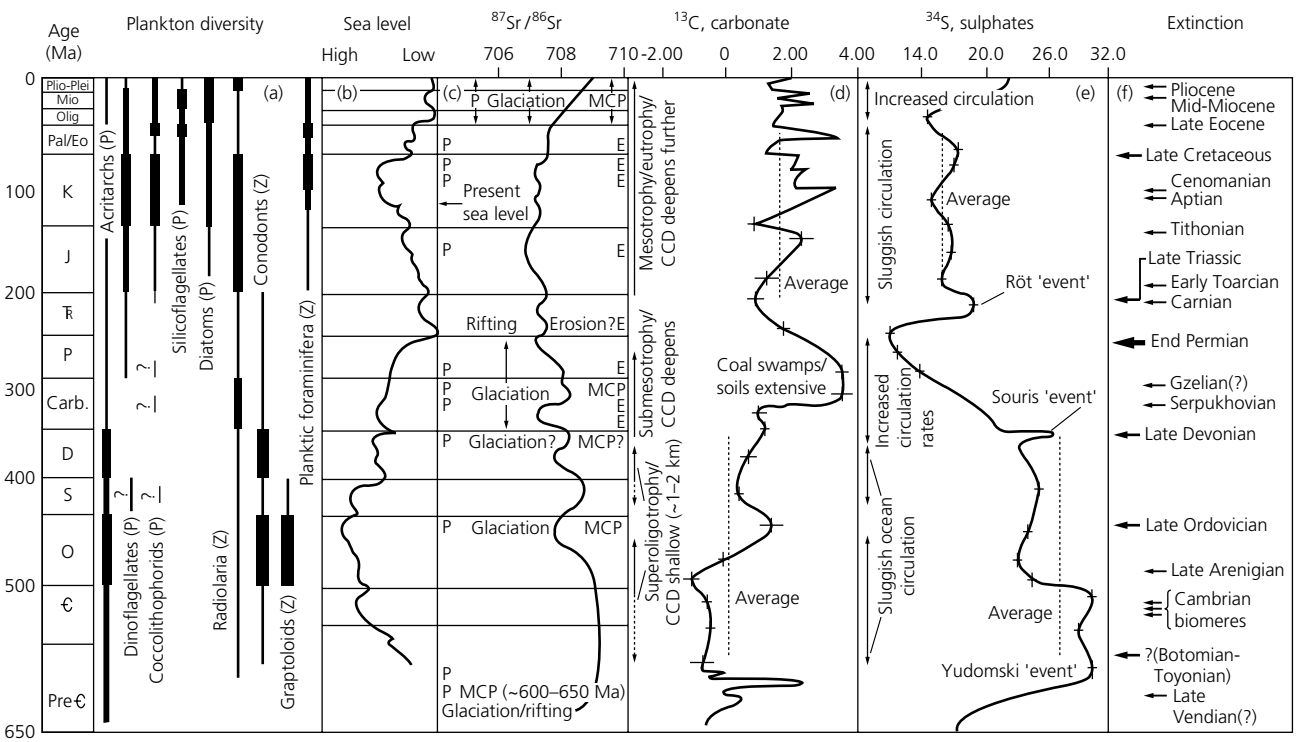


Fig. 3.3.4.1 Indices of ancient nutrient fluxes and productivity. (a) Relative diversity and abundance of microfossil taxa (period-averaged data); P, phytoplankton; Z, zooplankton (for simplicity, conodonts are considered to be zooplankton). (b) Sea level. (c) $^{87}Sr/^{86}Sr$ ratios; MCP, major eutrophication episodes; E, possible subsidiary eutrophication episodes; P, phosphorite peak. (d) Generalized $\delta^{13}C$ curve; *general* shift toward positive values through the Phanerozoic suggests heightened photosynthesis that resulted not only from expansion of terrestrial floras, but also from increased marine primary productivity as a result of increased marine C : P burial ratios during MCPs; averages (dotted lines) fitted visually. (e) Generalized $\delta^{34}S$ curve; 'events' may represent release into the photic zone of nutrient-rich waters previously stored in anoxic basins; Neogene $\delta^{34}S$ excursions may represent increased burial of C_{org} rather than anoxia; averages fitted visually. (f) Mass and minor extinctions; intensity indicated by arrows. (Modified from Martin 1996.)

('superoligotrophic' conditions of Martin 1996, 1998). Decreased rates of deep-ocean circulation, and a corresponding sequestration of nutrients below the photic zone, during the Cambro-Devonian are suggested by high $\delta^{34}S$ values, which in turn suggest extensive sulphate reduction in widespread anoxic basins: high $\delta^{34}S$ values indicate preferential reduction of the light isotope (^{32}S), thereby enriching sea water in ^{34}S (Fig. 3.3.4.1e; see Martin 1996, 1998 for alternative interpretations). Low rates of marine photosynthesis and organic carbon (C_{org}) burial are also suggested by the relatively light (negative) $\delta^{13}C$ values in marine carbonates: positive values indicate increased marine (or terrestrial) photosynthesis, whereas negative values indicate decreased productivity or oxidation of organic carbon sources (Fig. 3.3.4.1d).

Low phytoplankton densities during the Cambro-Devonian are also suggested by the record of acritarchs, which are probably marine eukaryotic unicellular algae that formed cysts in response to inimical conditions, perhaps including low nutrient availability. Thus, counter-intuitively, *high* acritarch (cyst) diversity prior to the Carboniferous (Fig. 3.3.4.1a) may reflect extremely *low* (not high) nutrient availability in the photic zone.

Fossil zooplankton also suggest adaptation to low phytoplankton densities during much of the Cambro-Devonian. Graptolites appear to have lived in low-oxygen, nutrient-rich waters, and may have migrated upward to feed on occasional phytoplankton blooms caused by intrusions of deeper nutrient-rich waters into the photic zone. Conodonts may have lived similarly, as they also exhibited depth stratification. Radiolarians apparently survived by living either in highly productive shallow waters, in oligotrophic (nutrient-poor) oceanic gyres with symbiotic algae, or in deeper subphotic layers of the open ocean as detritivores and bacterivores.

The presumed *overall* superoligotrophic surface conditions of the Cambro-Devonian were punctuated, however, by episodes of massive nutrient input to the photic zone during the late Precambrian–Early Cambrian, Late Ordovician, and Late Devonian. These episodes of increased marine C:P (MCP) burial ratios reflect increased nutrient availability and permanent enhancement of marine productivity and C_{org} burial rates (note positive shifts in $\delta^{13}C$ curve; Fig. 3.3.4.1d). MCP episodes often correspond to extensive phosphorite deposition that presumably resulted from one or more of the following: (1) intensified recycling of phosphorus back to the photic zone as a result of glaciation and enhanced ocean turnover of nutrient-rich deep water; (2) oxygenation of shallow waters and increased rates of bioturbation; (3) continental rifting and possible release of nutrient-rich waters (Yudomski and Souris $\delta^{34}S$ events; Fig. 3.3.4.1e); (4) orogeny and sea-level fall; and (5) increasing rates of weathering and soil formation, especially by the Late Devonian, as hinted by shifts in $^{87}Sr/^{86}Sr$ ratios (the greater the $^{87}Sr/^{86}Sr$ ratio, the greater the presumed influence of continental weathering and run-off) (Fig. 3.3.4.1c). Apparently, then, intervals of relatively low acritarch diversity reflect elevated *dissolved* nutrient levels immediately following the late Precambrian–Cambrian and Late Ordovician MCP episodes (i.e. abundant dissolved nutrients precluded cyst formation). Through the Cambrian and the Silurian, following the late Precambrian–Cambrian and the Late Ordovician MCP episodes, respectively, availability of dissolved nutrients presumably declined as nutrients were progressively incorporated into plankton (and other) biomass along food chains, so that acritarch diversity eventually rebounded to peak levels in the Ordovician and Devonian (returning to superoligotrophic conditions).

By the Carboniferous, nutrient availability had apparently reached a minimum threshold value ('submesotrophic' or subintermediate nutrient levels) that could support relatively large, permanent populations of plankton, thereby increasing the $CaCO_3$ pelagic rain and rates of C_{org} burial. The gradual shift in $\delta^{34}S$ to lower values suggests increased rates of ocean ventilation (and nutrient availability) as a result of Permo-Carboniferous glaciation. After the Late Devonian MCP episode, acritarch diversity remained quite low (most of the strong $\delta^{13}C$ shift in the Carboniferous and Early Permian was, however, probably the result of sequestration of C_{org} in terrestrial vegetation; Fig. 3.3.4.1d).

The Mesozoic–Cenozoic record of calcareous plankton

The diversification of marine plankton which began in the Mesozoic has typically been attributed to sea-level rise and the resultant increase in water-column stratification and habitat availability. $^{87}Sr/^{86}Sr$ and $\delta^{13}C$ values also began to rise following the end-Permian extinctions, however, suggesting that increased nutrient availability and enhanced marine primary productivity also promoted the rediversification of plankton (Fig. 3.3.4.1; cf. Röt event). Despite apparently sluggish ocean circulation during the Mesozoic (note $\delta^{34}S$ average; Fig. 3.3.4.1e), enhanced circulation (perhaps driven by salinity differences, wind, or submarine volcanism) at times may have stimulated dramatic rises in marine productivity; indeed, extensive phosphorites sometimes occur in the vicinity of oceanic anoxic events that are associated with extensive C_{org} burial. Nutrient cycling on shelves through the Mesozoic may also have accelerated in response to rising bioturbation rates (because of increased food – C_{org}– in sediment) and, by the Cretaceous, to the expansion of angiosperms, since

angiosperm leaf litter decays more rapidly than that of gymnosperms, which dominated most of the Mesozoic.

The record of Mesozoic marine plankton also suggests that nutrient availability surpassed that of the Palaeozoic. Among the dominant groups of Mesozoic plankton are the dinoflagellates (Fig. 3.3.4.1a), the modern representatives of which tend to prefer mesotrophic (intermediate) nutrient levels. Dinoflagellates have sometimes been allied with acritarchs because they form cysts. Unlike acritarchs, however, the diversification of dinoflagellate cysts during the Mesozoic would appear to signal *heightened* nutrient levels. Strong positive $\delta^{13}C$ excursions and MCP boosts began again in the Cenozoic, near the Eocene–Oligocene boundary. These shifts reflect increased marine productivity as a result of formation of polar ice caps, enhanced deep-water overturn, and continental erosion (through sea-level fall) and nutrient input from land (note $^{87}Sr/^{86}Sr$ curve; Fig. 3.3.4.1c).

Siliceous oozes

Like calcareous oozes, deposition of siliceous oozes shifted across the shelf during the Palaeozoic, although siliceous preceded calcareous oozes by several hundred million years in the fossil record (Fig. 3.3.4.1a). In the Cambrian, biogenic cherts were predominantly shallow subtidal and the by-product of evolutionary diversification of demosponges and problematic siliceous scale-producing protists (Maliva *et al.* 1989). After the rise of radiolarians in the Cambro-Ordovician, the locus of siliceous ooze deposition began to shift across the shelf to the open ocean. Beginning in the Mesozoic and continuing to the Neogene, radiolarians began to give way to silicoflagellates and (especially) diatoms, which prefer eutrophic (nutrient-rich) conditions. In contrast to the robust appearance of Palaeozoic radiolarians, their Mesozoic counterparts formed lattice-like skeletons, perhaps as a result of competition with diatoms for dissolved silica. Although the oldest reliable record of diatoms is Jurassic (Toarcian), spindle-shaped (pennate?) diatom-like structures from late Proterozoic stromatolitic carbonates have been reported. *If* diatoms existed prior to the Jurassic, their apparent absence from open oceans during the Palaeozoic and early Mesozoic may indicate their restriction to nearshore, highly nutrient-rich habitats, in which fragile siliceous shells are unlikely to have been preserved.

Summary

The record of marine plankton suggests that organic carbon burial rates increased through the Phanerozoic. Likewise, metabolic levels of marine taxa increased as they became progressively acclimatized to increasing food availability through the Phanerozoic, and the length of food chains and the complexity of food webs increased accordingly (Bambach 1993; Martin 1996, 1998). Perhaps, then, the three eras of the Phanerozoic should be referred to as the 'Oligozoic', 'Mesozoic', and 'Euzoic', respectively.

Ironically, and contra 'Strangelove Oceans', fluctuations in resource levels may have augmented Palaeozoic mass extinctions by stimulating blooms of opportunistic plankton that destabilized ecosystem structure (Fig. 3.3.4.1). Following each of the extinctions, however, heightened nutrient availability and MCP burial ratios fuelled re-expansion of biodiversity and biomass to levels greater than those preceding extinction, and, as a result, there was a concomitant decline in background extinction rates through the Phanerozoic. This property was immanent in opportunistic taxa because they tended to survive catastrophes, reproduced rapidly, and founded many new taxa during postextinction recoveries.

References

Bambach, R.K. (1993) Seafood through time: changes in biomass, energetics, and productivity in the marine ecosystem. *Paleobiology* **19**, 372–397.

Boss, S.K. and Wilkinson, B.H. (1991) Planktogenic/eustatic control on cratonic oceanic carbonate accumulation. *Journal of Geology* **99**, 497–513.

Maliva, R.G., Knoll, A.H. and Siever, R. (1989) Secular change in chert distribution: a reflection of evolving biological participation in the silica cycle. *Palaios* **4**, 519–532.

Martin, R.E. (1996) Secular increase in nutrient levels through the Phanerozoic: implications for productivity, biomass, and diversity of the marine biosphere. *Palaios* **11**, 209–219.

Martin, R.E. (1998) *One long experiment: scale and process in Earth history*. Columbia University Press, New York.

3.3.5 Terrestrial Plants

R.A. GASTALDO

Introduction

Terrestrial plants can be considered equivalent to the sessile benthos of the marine realm. As such, assemblages of fossil plants share many traits with those of marine animals, particularly in the origination of whole plant and plant-part accumulations. In dramatic contrast

to most animals, however, plants do not have to die to contribute biomass to the stratigraphic record. Other differences that affect the taphonomy of plants include the absence of a crystalline skeletal organization, the possession of an array of different cellular components organized into a variety of architectural plans, a wide range of biological strategies to overcome stresses associated with life on land, and interactions with physical processes other than those in the marine realm (Gastaldo 1992). Terrestrial settings are primarily sites of erosion; hence, fossil plant assemblages are restricted mainly to sites of sediment accumulation where narrowly constrained physicochemical parameters are met on a short-term basis (Spicer 1989; Gastaldo 1994). Unlike many marine and terrestrial faunal assemblages, fossil plant assemblages are not time-averaged (see Section 3.2.7), but a snapshot that represents a short duration of geological time (10^0–10^2 years; Burnham 1993).

Life strategies

Plants are primary producers, anchoring the food chain. Constrained to undergo an alternation of generations to complete their life cycle, two strategies evolved during the Phanerozoic that allowed plants to inhabit nearly every imaginable terrestrial realm. The *r-strategists*, or opportunists, invest little in long-term root and shoot (vegetative) growth and development of a diploid ($2n$) sporophyte. These plants grow rapidly, are determinate (i.e. reproduction occurs after vegetative growth to a preprogrammed developmental state, generally in less than one to a few years), and disseminate or produce large quantities of male and female reproductive structures. *K-strategists*, on the other hand, invest large amounts of energy in the production of sporophyte vegetative biomass. These plants grow more slowly (and can attain ages of several hundred to thousands of years), are indeterminate (i.e. reproductive phases alternate with vegetative growth phases during the course of a growing season), and generally produce large quantities of vegetative biomass that are shed to the environment with less expenditure committed to reproduction. Hence, there is a difference in the probability of preserving a representative from either life strategy, even when the physicochemical conditions for preservation are met (Gastaldo 1992). Plant parts that originate from *K*-strategists have a higher probability of being preserved in the plant fossil record under a variety of depositional conditions; plant parts that originate from *r*-strategists have a very low probability of being preserved unless buried *in situ* by a catastrophic event (Fig. 3.3.5.1).

The generalized plant body comprises: (1) a buried, subterranean axial system (rhizome in the lower vascular plants; roots in higher vascular plants); (2) an aerial nonwoody or woody axis with or without lateral branches; upon which (3) photosynthetic organs originate (leaves

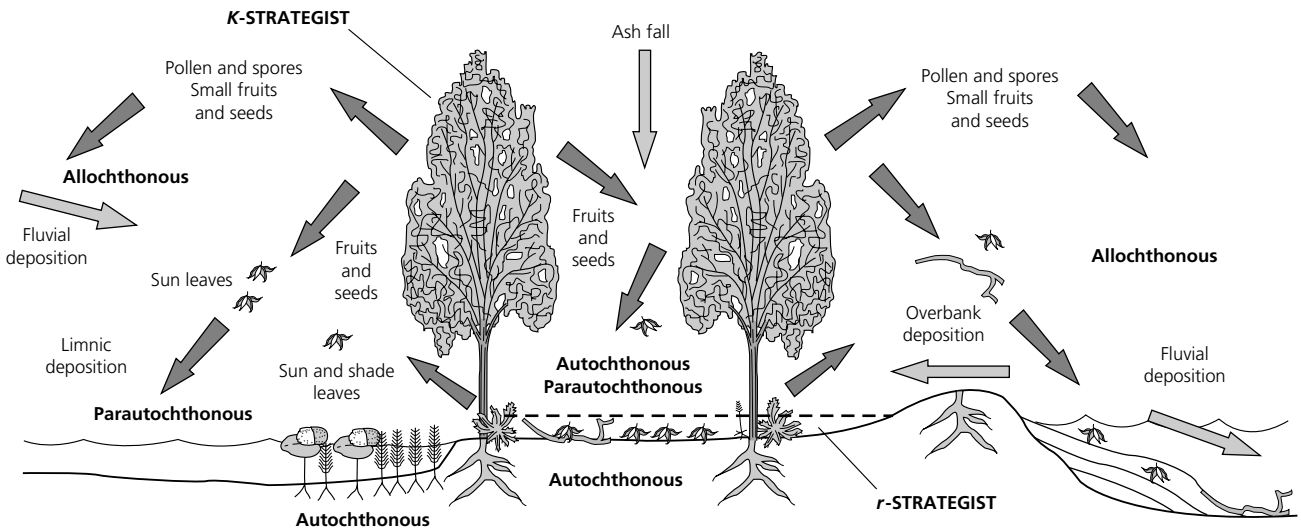


Fig. 3.3.5.1 Schematic transect across a terrestrial landscape from lacustrine to fluvial environments on which *r*- and *K*-strategists coexist. Contribution to potential fossil assemblages may result from physiological or traumatic loss (Gastaldo 1992). Autochthonous assemblages may be preserved at lake margins, within alluvial soils (palaeosols; Retallack 1990) or above soils as peat mires, or as litters buried by catastrophes (ash fall or high-discharge, low-frequency overbank events; Spicer 1989). Parautochthonous assemblages may be preserved in proximal parts of small lakes, at the lake margin (where submerged and semiaquatics do not prevent accumulation at the sediment–water interface), within the alluvial floodplain, or in forebank deposits (Burnham 1993). Allochthonous assemblages can develop in distal parts of large lakes, in delta deposits where rivers or streams empty into a lacustrine setting, within channel bars and lag deposits of river systems, deltaic distributaries and mouth bars, and in offshore shelf settings (Gastaldo 1994).

or other photosynthetic axes); along with (4) reproductive structures (naked sporangia associated with axes or leaves, cones, or flowers); in which are produced (5) reproductive propagules (spores, pollen [male gametophytes], ovules [female gametophytes]); that upon fertilization result in embryos that may be protected within (6) seeds and fruits (Fig. 3.3.5.1). Each of these organs has a different probability of preservation that is controlled, in part, by cellular biochemical properties (Gastaldo 1994) and the environment in which the plant lives or into which the parts are disseminated.

Rooting systems

Where subterranean rhizomes and rooting systems are preserved, they are generally (but not always) indicative of autochthonous (preserved in growth site) communities that inhabited an undifferentiated or differentiated soil. Palaeosols vary in their physical and chemical characteristics which are, in part, a product of the vegetation that grew and modified these sediments (Retallack 1990). Rooting structures in wetland soils have a higher probability of preservation, due to porewater chemistry, than sites in which the water table fluctuates. Resistant fruits, seeds, and opaline phytoliths may be recovered from a variety of soil types, and are either autochthonous or parautochthonous (preserved within the community but not at the exact site of growth).

Aerial parts

Non-woody and woody (lignified) aerial axes can be preserved *in situ* under catastrophic event deposition such as high-discharge, low-frequency overbank flooding (e.g. the Fossil Grove, Glasgow) or tephra ash fall (e.g. Yellowstone Tertiary forests; Spicer 1989). Leaf litters buried along with standing communities reflect canopy, understorey, and ground-cover contributions that range in age from weeks to several years (flowers, leaves, small branches and bark, cones, fruits and seeds) to a century or more (i.e. woody trunks; Burnham 1993). Rooting systems of woody trunks can be undercut and introduced into fluvial (via cutbank erosion or mass wasting) and marine (via tidal and/or wave erosion) environments. Coarse woody debris can then be transported away from its growth site (allochthony), become waterlogged and sink (unless initial wood density is >1, when sinking is immediate), and ultimately may be buried (Gastaldo 1994). Allochthonous fluvial assemblages may result in river system modification due to the accumulation of log jams (e.g. Red River, Louisiana), or they may become woody substrates for marine invertebrates in shelf settings.

Photosynthetic leaves

Although *K*-strategists can be evergreen or deciduous, leaves are always shed once they become non-functional (physiological loss; Greenwood 1991) or are affected by traumatic events (e.g. hurricanes, drought, volcanic eruptions; Gastaldo 1992). Their decomposition has been investigated in modern field (forest floor, lake, river, and delta) and laboratory settings with respect to biological (bacteria, fungi that predispose organic matter to attack by invertebrates) and physical influences (Greenwood 1991). Preservation potential is enhanced by bacterial colonization and the production of a biofilm, although leaf litter preservation in peat swamps may be more a function of pH and Eh relationships in subsurface waters. Nevertheless, a single bed of fossilized leaves represents a very narrow window of time, most probably less than 3 years (inclusive of growth on the parent plant; Burnham 1993), even when encountered in allochthonous assemblages. Transported waterlogged leaves fragment when reworked by mechanical processes, resulting in the formation of phytoclasts (Gastaldo 1994) often referred to as 'comminuted debris'.

Autochthonous leaf assemblages provide a high-fidelity record of the original community structure, while parautochthonous and allochthonous assemblages buried in lakes and rivers, respectively, demonstrate a bias towards outer canopy (sun) leaves of marginal (riparian) vegetation. Leaves introduced into an aquatic setting exhibit a wide range of float times during which they can be transported distances of more than 50 km (depending upon the physical characteristics of the water body; Gastaldo 1994).

Reproductive structures

Produced in abundance, reproductive structures (sporangia, cones, flowers) are short-lived (days to weeks) ephemeral organs that have a low probability of preservation unless affected by traumatic processes (e.g. wildfire and charcoalification; see Section 3.2.3). The reproductive propagules that develop within them, however, have evolved properties that allow them to remain viable for much longer periods of time (10^1–10^2 years). Spore and pollen walls are composed of resistant biopolymers, such as sporopollenin and chitin, ensuring a biochemical bias towards their preservation in a wide variety of terrestrial and marine settings. In general, most pollen and spores accumulate within the broad confines of the community of origin (including those disseminated by animals), although dispersal by wind and water may result in the distribution of some pollen types several thousand kilometres from their site of origin.

Seeds and durable fruits can possess lignified cell

walls that resist mechanical and microbial decay, and which thereby protect the embryo for intervals that can exceed 10^3 years (oldest known viable seeds >5 kyr). 'Acorns don't fall far from the parent' and, as such, autochthonous accumulations referred to as 'seed banks' can be found in palaeosols. These organs also can be subjected to a wide variety of dispersal mechanisms (animals, wind, and water), however, resulting in the concentration of hydrodynamically equivalent structures in aquatic settings. The fact that many durable fruits and seeds are buoyant allows them to be dispersed along coastlines for distances greater than 1000 km from their parent community (depending upon prevailing ocean currents). Under unusual and poorly understood circumstances, fruits and seeds may be concentrated into thick beds (e.g. London Clay) that may be time-averaged on the order of 10^2 years (Burnham 1993) or more.

Development of fossil assemblages

The incorporation of plants and plant parts into the sedimentary record depends on: the growth periods and life strategies of the source vegetation; the physiological and/or traumatic production of organic debris (necrology) that may accumulate and be subjected to early diagenetic processes (biostratinomy); and burial and integration into the rock record (diagenesis). The complex factors involved in the production of a fossil plant assemblage result in the temporally fragmentary nature of the Phanerozoic plant record. Nevertheless, once preservational biases associated with different plant organs are understood, this fragmentary record can be used to evaluate trends in evolutionary innovation, ecosystem dynamics, biogeochemical cycles, and hydrocarbon resources.

References

Burnham, R.J. (1993) Time resolution in terrestrial macrofloras: guidelines from modern accumulations. In: S.M. Kidwell and A.K. Behrensmeyer, eds. *Taphonomic approaches to time resolution in fossil assemblages*, pp. 57–78. Short Courses in Paleontology, no. 6. The Paleontological Society, Knoxville, Tennessee.

Gastaldo, R.A. (1992) Taphonomic considerations for plant evolutionary investigations. *Palaeobotanist* **41**, 211–223.

Gastaldo, R.A. (1994) The genesis and sedimentation of phytoclasts with examples from coastal environments. In: A. Traverse, ed. *Sedimentation of organic particles*, pp. 103–127. Cambridge University Press, Cambridge.

Greenwood, D.R. (1991) The taphonomy of plant macrofossils. In: S.K. Donovan, ed. *Fossilization: the process of taphonomy*, pp. 145–169. Columbia University Press, New York.

Retallack, G.J. (1990) *Soils of the past: an introduction to paleopedology*. Unwin Hyman, Boston, Massachusetts.

Spicer, R.A. (1989) The formation and interpretation of plant fossil assemblages. *Advances in Botanical Research* **16**, 95–191.

3.3.6 Pollen and Spores

J.M. VAN MOURIK

Introduction

Pollen grains and spores, both recent and ancient, are useful in a range of scientific studies based on palynological extracts from different sources. Studies of recent pollen morphology are based on grains removed from stamens, which are unaffected by any deterioration process. Studies of vegetation history and climatic change are based on ancient pollen from aquatic sediments and peat. Investigations of archaeology and landscape ecology may also be based on ancient pollen, extracted from humic soil horizons. Pollen is subject to deterioration during the interval between its liberation from the stamen and its incorporation into sediment or soil. The most common processes are corrosion, degradation, and mechanical damage. Pollen corrosion is caused by microbial attack, by fungi and bacteria, which results in perforation of the exine. Degradation is caused by chemical oxidation, which leads to thinning rather than perforation. Both corrosion and degradation are promoted by drainage and aeration of the enclosing sediment. Mechanical damage is caused by physical agents, like shrinkage and swelling of soil, which result in crumpling or rupturing of the exine. Damage also occurs during transport by wind and insects, and as a result of consumption and redistribution by soil invertebrates. Last but not least, the methods used to extract pollen and spores for study also contribute to their deterioration.

Complexity of pollen spectra

Pollen grains of various plant species show typical microscopic characteristics (aperture and sculpture) and can be identified systematically (Moore *et al.* 1991). A *pollen spectrum* is the result of the taxonomic determination of a pollen extraction, expressed in pollen types and frequencies. The interpretation of pollen spectra requires a knowledge of pollen productivity and dispersal for the various species encountered. In general, wind-pollinated species are over-represented and insect-pollinated species under-represented. The interpretation of fossil pollen spectra also requires an understanding of the processes of pollen incorporation into sediments and soils, and subsequent preservation. The microenvironment within sediments or soils can affect the preservation quality and even the types of pollen represented. Experiments on the deterioration of pollen grains in litter bags (Havinga 1984) have shown that differences in

the chemical composition of the exine affect their preservation potential. The percentage of resistant pollen species in soil increases relative to those more prone to deterioration, while some species do not fossilize at all.

Synsedimentary pollen precipitation

The pollen content of peat and lake deposits is considered to be synsedimentary. Preservation is promoted in water-saturated deposits due to anaerobic conditions. Temporary or permanent drainage, on the other hand, results in the deterioration or even complete destruction of pollen grains, by corrosion and degradation. In rainwater-controlled moorlands the water table is relatively stable, and peat accumulates rapidly. Pollen is incorporated into the water-saturated organic sediment, and deterioration is inhibited. The water table of groundwater-controlled peat moors is less stable, resulting in more rapid decomposition of organic litter and greater deterioration of pollen by corrosion and degradation. Thin sections reveal how free pollen grains occur in a sedimentary matrix, composed of organic or mineral particles (Fig. 3.3.6.1). The pollen content of lacustrine deposits is well preserved while conditions remain water saturated, but following drainage and aeration the grains oxidize completely.

Postsedimentary pollen infiltration

The pollen content of terrestrial humic soil horizons is postsedimentary. The aerobic conditions of well-drained soils promote corrosion and degradation of free pollen grains (not protected from oxidation). The interpretation of soil pollen spectra, based on extractions of embedded grains (well protected from oxidation), requires an understanding of the processes that control the infiltration, incorporation, and preservation of pollen grains in soil. In thin sections of undisturbed soil samples, pollen and spores can be identified as sporoid bodies. Taxonomic identification of the grains is impossible because the surface of the exine is not cleaned during preparation and may even be hidden by fine organic and mineral soil particles. The micromorphological setting of the pollen grains, however, gives information about their incorporation into the soil and conditions of preservation.

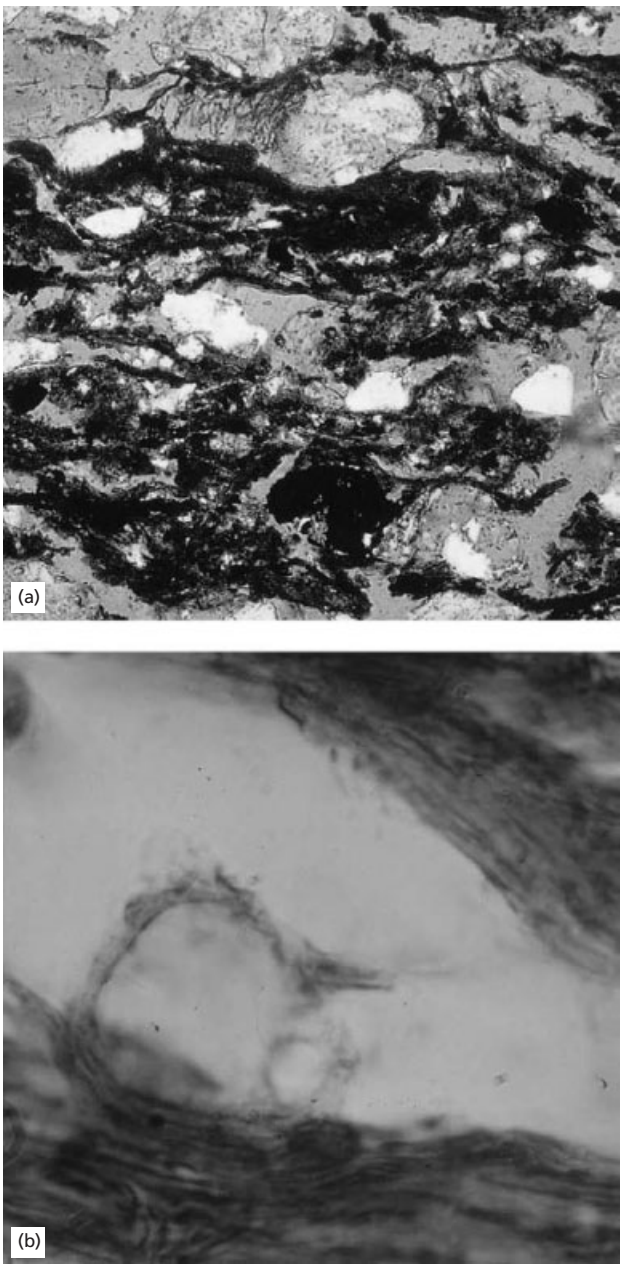


Fig. 3.3.6.1 Allerød peat. (a) Matrix composed of litter of *Scorpidium scorpioides* and fine wind-blown sand, ×75. (b) Free pollen grain embedded in water-saturated organic litter, ×1190.

Pollen infiltration controlled by the soil fauna

The pollen zonation of acid soils reflects local landscape-ecological change (Dijkstra and Van Mourik 1995; Davidson *et al.* 1999). Pollen is deposited as part of the organic litter on a soil surface. Water does not transport pollen into the soil; pollen grains have hydrophobic properties and the mean grain size does not allow vertical transport of single grains through soil pores (Van Mourik 1999). Micromorphological observations show that pollen is present in faecal pellets produced by soil invertebrates, but never in voids or channels (Van Mourik 1999). Single pollen grains only occur outside faecal pellets in the very young organic horizons of humus profiles (Dijkstra and Van Mourik 1995). Thus soil biological activity is an important factor in the infiltration and preservation of pollen in soil horizons. After deposition, litter is subjected to microbial decom-

position. Depending on the source vegetation, the litter may consist of a range of tissues, with various C/N-values, which are decomposed by different soil organisms at various rates.

In chemical-rich (eutrophic) ecosystems, the protein content of the litter is high (C/N-value <15). Fresh litter is fermented and decomposed primarily by humus-forming animals such as microarthropods. They consume and digest litter, including bacterial mucus, fungi, and pollen. The walls of pollen grains are not digestible and are incorporated into the faeces. This dense acidic microenvironment protects pollen against microbial attack and deterioration, but promotes mechanical damage. The excrement of primary consumers is the main source of food for saprophagous soil animals such as earthworms. They live mostly in the humus profile and penetrate partly into the mineral soil. They are of great importance for the dispersion of pollen through the soil profile (Walch *et al.* 1970). Primary and secondary consumers are together responsible for the development of a vermimull humus form, characterized by a mixture of organic and fine mineral particles, produced by earthworm activity and secreted in channels in the mineral soil (Fig. 3.3.6.2a). In thin sections pollen grains can be observed in earthworm excrement (Fig. 3.3.6.2b).

In less chemical-rich (mesotrophic) ecosystems the protein content of the litter is low (C/N-value >15), and decomposition is restricted to humus-inhabiting soil animals and fungi. This activity results in the development of a mormoder humus form, a concentration of fine organic material, mainly excrement, produced by microarthropods in the organic horizon (Fig. 3.3.6.3a). In thin sections pollen grains can be observed in organic aggregates (Fig. 3.3.6.3b). The gradual acidification of the ecosystem causes a reduction in the activity of the soil fauna, resulting in a zonation of the soil pollen profile.

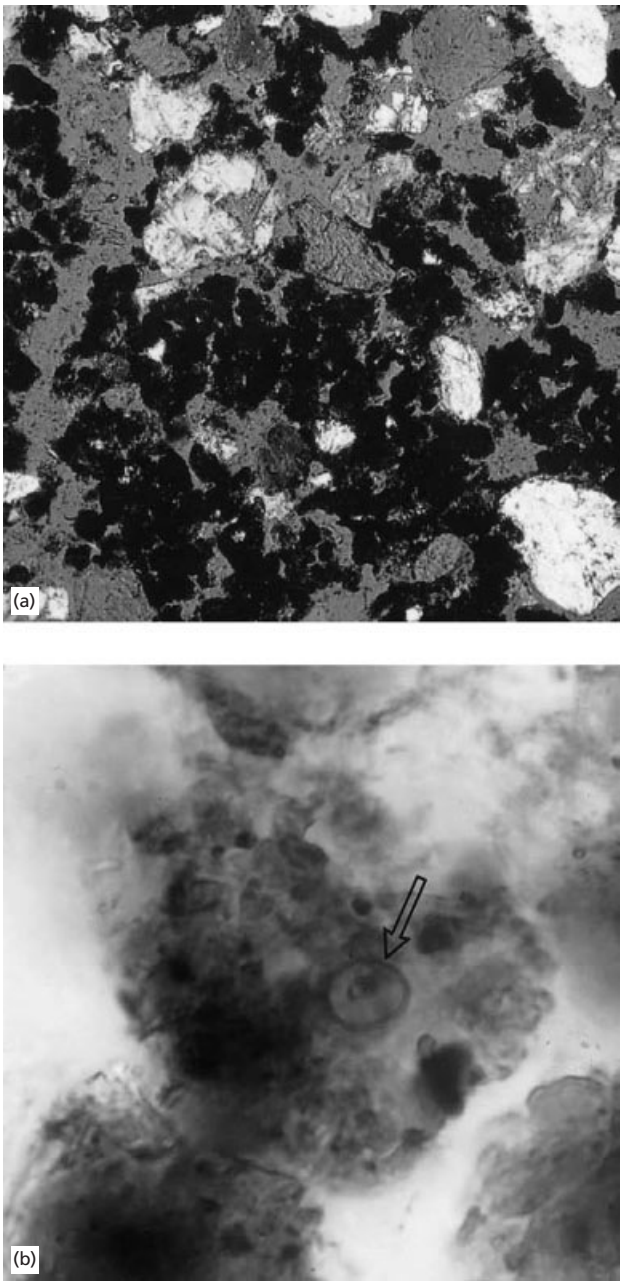
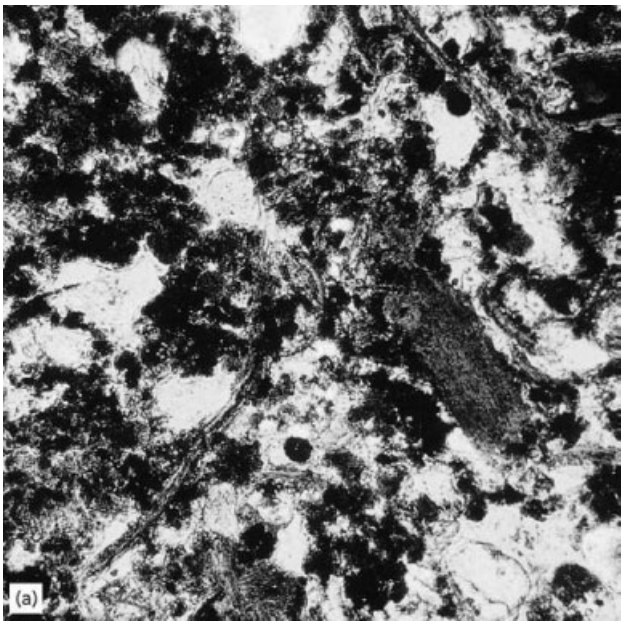


Fig. 3.3.6.2 Vermimull humus form. (a) Matrix showing the distribution of excrement produced by soil invertebrates in the mineral soil, ×75. (b) Pollen grain (indicated by arrow) incorporated in earthworm excrement, ×570.

Palyno-ecological 'fingerprints'

Pollen grains are subjected to corrosion and degradation in the interval between aeolian deposition and excretion by soil organisms. During the complex cycle of consumption, excretion, and decay of organic matter by the soil fauna, pollen grains and spores are subjected to intensive mechanical damage. Soil pollen spectra are useful ecological 'fingerprints' for archaeological and landscape-ecological studies. The contrast between the pollen-producing species represented in spectra (following the taphonomic processes described above) and the composition of the standing vegetation restricts their application in studies of vegetation or climatic history.

Palynological preparations from soil materials are rich in spores. In contrast to the pollen, which is introduced, spores are produced mainly *in situ* in the soil. Microorganisms, mainly fungi, play an important role in decomposition. They transform organic matter into inorganic components (e.g. CO_2 and H_2O) and humus. Some fungi live on the subaerial parts of plants. The spores of these fungi contribute to the normal aeolian pollen, and are incorporated into the soil in the same way. Most fungi, however, decompose organic matter in the organic hori-



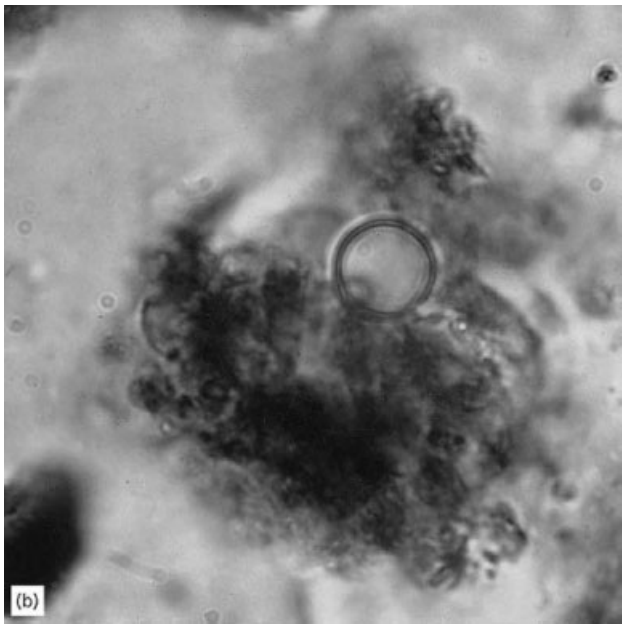


Fig. 3.3.6.3 Mormoder humus form. (a) Matrix developed under Scots pine by fermentation of litter controlled by microarthropods, ×75. (b) Pollen grain embedded in agglomerated faecal pellets of larger arthropods (in the fermentation horizon); pollen grains are too big to be consumed by small arthropods, but are incorporated in the faecal pellets of older individuals, ×570.

zons of soil, where temperature and moisture content are more favourable. Soil fungi (usually ascomycetes and deuteromycetes: Fungi Imperfecti) are mainly responsible for the decomposition of cellulose, lignin, and chitin. Most of these fungi are saprophytes (i.e. they are free in the soil), but a minority are parasitic or semiparasitic on plant roots. Another important group of saprophytic fungi, the basidiomycetes, live with their mycelia in the soil. Otherwise they occur as dormant stages—spores (conidia) or chlamidospores. Spores and other remains of fungi can be identified in palynological preparations. The spores produced *in situ* are not precisely contemporaneous with infiltrated pollen grains. Nevertheless, spore associations are indicative of particular environments, and an analysis of spore content can contribute to the ecological fingerprint of a soil (Dijkstra and Van Mourik 1995).

References

Davidson, D.A., Carter, S., Boag, B., Long, D., Tipping, R. and Tyler, A. (1999) Analysis of pollen in soils: processes of incorporation and redistribution of pollen in five soil profile types. *Soil Biology and Biochemistry* **31**, 643–653.

Dijkstra, E.F. and Van Mourik, J.M. (1995) Palynology of young acid forest soils in the Netherlands. *Mededelingen Rijks Geologische Dienst* **52**, 283–296.

Havinga, A.J. (1984) A 20-year experimental investigation into the differential corrosion susceptibility of pollen and spores in various soil types. *Pollen and Spores* **26**, 541–558.

Moore, P.D., Webb, J.A. and Collinson, M.E. (1991) *Pollen analysis*, 2nd edn. Blackwell Scientific Publications, Oxford.

Van Mourik, J.M. (1999) The use of micromorphology in soil pollen analysis. The interpretation of the pollen content of slope deposits in Galicia, Spain. *Catena* **35**, 239–257.

Walch, K.M., Rowley, J.R. and Norton, N.J. (1970) Displacement of pollen grains by earth worms. *Pollen et Spores* **12**, 39–45.

3.3.7 Terrestrial Vertebrates

A.K. BEHRENSMEYER

Introduction

Vertebrates have a relatively large skeletal mass consisting of several hundred identifiable bones per individual and thus have an advantage in numbers of preservable parts compared with shelly macroinvertebrates. However, for terrestrial vertebrates, this advantage is outweighed by the fact that their populations are relatively small, highly mobile, and often widely dispersed across the land surface. Consequently, they have provided much less total biomass to the fossil record than plants or invertebrates. Preservation of individuals or

concentrations of remains requires particular taphonomic processes and circumstances that also introduce significant biases into how these remains represent the once-living populations or communities. These processes and circumstances are determined by the ecological setting of life, death, and preservation.

Early research in the taphonomy of terrestrial vertebrates concentrated on the physical and biological transport of bones as a source of bias in the fossil record. Subsequent investigations revealed how other processes affect biological and ecological information in assemblages of fossilized vertebrate remains. There is now increased understanding of the interconnected effects of environment of deposition, physical transport, body size, time-averaging, bone-collectors, and chemical alteration before and after burial. Many recent taphonomic studies have focused on dinosaurs and other large-bodied terrestrial groups, resulting in new information about the preservational history of nesting sites, trackways, mass bone accumulations, and Lagerstätten with preservation of soft as well as bony remains (see Section 3.4).

Environment of deposition

Vertebrate remains are rare in the context of the entire fossil record, but they are predictably present in many depositional settings and can be extraordinarily abundant. What we know about vertebrate palaeobiology is strongly affected by the depositional environments that preserve high-quality records of individual species and species associations through time. The patterns of occurrence of terrestrial vertebrate remains depend on: (1) the types of sediments that preserve such remains; (2) how abundant the remains are in these sediments; and (3) the frequency of these sediments in the geological record.

For most of the Phanerozoic, vertebrate remains probably have occurred in every major land environment. However, physical, chemical, and biological processes that recycle bones prior to or shortly after burial left a fossil record only in particular places within the terrestrial setting. Land vertebrates are most often present in fluvial and lacustrine depositional environments (Behrensmeyer and Hook 1992) (Table 3.3.7.1). Within fluvial deposits, remains occur in coarse-grained channel bars (including point bars), coarse- to fine-grained channel fills (including abandoned channels and oxbows), crevasse-splays, and floodplain soils. Patterns of preservation across these subenvironments vary in different fluvial sequences as a consequence of rates and modes of fluvial aggradation and climate (Smith 1993; Badgley and Behrensmeyer 1995). Lacustrine deposits preserve terrestrial as well as aquatic vertebrates in deep to shallow water settings (including lake margin and deltaic facies). Land vertebrate remains are also known in volcanigenic deposits, coastal environments (such as beaches, lagoons, and estuaries), aeolian dunes, interdunes and loessic silts, and a range of unusual settings including tar seeps, amber, caves, sinkholes, fissures, springs, packrat middens, and archaeological sites (for complete listing, see Behrensmeyer and Hook 1992).

These burial environments provide a wide range of temporal and spatial samples of the original vertebrate

Table 3.3.7.1 Environmental settings that preserve the land vertebrate fossils, with a qualitative assessment of the richness of the vertebrate record from each setting in different parts of the Phanerozoic. The relative frequency of the settings is indicated by: +++, very common; ++, common; +, present; (+), rare; –, very rare to absent. In the Pleistocene–Recent column, this shows that fluvial/deltaic settings are most common and tar seeps and amber least common. Coding in the other two columns indicates the importance of each environment as a source of vertebrate remains in earlier time periods, relative to its frequency in the Pleistocene–Recent. (Modified from Behrensmeyer and Hook 1992.)

Environmental setting	Pleistocene–Recent	Pre-Pleistocene Cenozoic	Mesozoic–Palaeozoic
Marine coastal	+	+	(+)
Fluvial/deltaic	+++	+++	+++
Lacustrine	++	++	+
Volcanic	+	++	+
Aeolian	+	+	+
Other small-scale contexts			
Tar seeps	++	–	–
Amber	(+)	(+)	–
Karst (caves, fissures, etc.)	++	+	(+)
Springs	+	(+)	–
Middens	+	–	–
Burrows	+	+	+
Archaeological sites	++	–	–

communities. They provide valuable insights about past ecology, but misinterpretations can occur when species indigenous to one habitat are buried in another, or when species that did not live together, either in a temporal or spatial sense, were buried together. Small-scale sites, such as abandoned channels and tar seeps, preserve animals that inhabited the local ecosystem but may time-average faunas over periods of 10^3–10^4 years. Thus, if short-term environmental shifts occurred within this time interval, species may be buried together that did not live together. Floodplain soils represent larger-scale spatial samples of animals that lived in the floodplain habitat but may also time-average vertebrate remains (Behrensmeyer and Hook 1992; Graham 1993). Channel lag and bar assemblages combine skeletal remains from all the fluvial subenvironments because these remains are eroded from pre-existing deposits as well as introduced directly into the channel. Such assemblages thus are more likely to represent the fauna from the fluvial system as a whole rather than any particular subhabitat.

Quality and abundance of vertebrate remains

Articulated complete skeletons represent optimal preservation for individual vertebrates, and such occurrences are uncommon but present in all of the environments listed above. In some cases skeletons may include soft-part impressions or, rarely, three-dimensional replicas of tissues and organs (see Section 3.4.8). Fossils of this kind provide a maximum amount of information on functional morphology and may be amenable to analysis of fossil biomolecules (see Section 3.1). The highest-quality preservation typically occurs in local settings where there was rapid burial with minimal disruption by scavengers; soft parts are preserved only under highly favourable conditions of water chemistry and bacterial activity.

Most of the vertebrate record consists of fragmentary remains, especially teeth and other biomineralized elements, such as dermal scutes and enameloid scales. When these remains are identifiable to genus or species, they are more useful as a record of vertebrate evolution and palaeoecology than the rare occurrences of complete specimens. Differential preservation of body parts is characteristic of environmental settings where taphonomic processes have time to interact with remains prior to burial. In fluvial, lacustrine, coastal, and some aeolian settings, predators and scavengers are active soon after the death of an animal and typically damage, disperse, and destroy small and low-density skeletal parts, as well as those that are meat-bearing (e.g. limb elements). These taphonomic processes bias the record toward more robust bones and against small, lightly built (e.g. birds), and juvenile remains (Behrensmeyer 1991). Transport of bones may cause biases with respect to body size when small elements are separated from large ones by current action. Flowing water also tends to separate lighter from heavier elements, burying teeth, jaws, and limb parts as a 'lag' assemblage, while the more buoyant and transportable vertebrae, ribs, and cranial parts are subjected to dispersal, exposure, and destruction. These processes, combined with time-averaging, result in fossiliferous deposits dominated by disarticulated, broken, and often size-sorted remains as samples of the species that inhabited all or part of the original environment (e.g. fluvial drainage system, dune field, coastal plain).

In contrast to the broad environments described above, tar pits, caves, fissures, springs, middens, and archaeological sites are small-scale spatial settings strongly affected by biological processes, i.e. habitat preference, predation, scavenging, and bone-collecting. These processes can result in extraordinary densities of fragmentary remains accumulated over relatively long periods of time (10^2–10^4 years) (Behrensmeyer and Hook 1992; Graham 1993). Caves and fissures tend to preserve small animals that occupy such habitats or are transported there by predators such as owls and leopards. Body size, species present (e.g. nocturnal vs. diurnal), and damage patterns are strongly related to the type of predator (Andrews 1990). Such assemblages typically represent 'upland' environments and may sample a different vertebrate community than lowland depositional settings. Trap situations (quicksand, mud, peat bogs, sinkholes, springs, tar pits) contain high concentrations of associated or isolated bones dominated by species that were susceptible to trapping (e.g. large ungulates). In the special case of tar pits, bones are usually complete but disassociated by the internal flow of the tar, and the fauna contains a disproportionate number of predators and scavengers that were attracted to other trapped animals. Archaeological sites often contain significant concentrations of vertebrate remains that represent the activities of hominids and other bone-collecting or dispersing agents. These sites occur in all major environmental settings and may be time-averaged over relatively short intervals (10^1–10^2 years).

Patterns through geological time

Vertebrate-preserving deposits are distributed unevenly through time, reflecting global- to regional-scale tectonic and climatic processes (Table 3.3.7.1). Fluvial and fluviodeltaic deposits with vertebrate remains are relatively common throughout the terrestrial record and represent the most continuous samples from specific environmental settings. Other types of terrestrial deposits are poorly represented in the older record because few of them survive long-term processes of continental erosion and plate tectonics. Lacustrine and volcanigenic deposits are common in the Cenozoic but are preserved mainly in

rift valley contexts or lowland fluvial systems in the Mesozoic and Palaeozoic. Tar pits, springs, caves, and fissures are rare in the pre-Pleistocene record, although examples of vertebrates in fissure fills occur as far back as the Devonian (Behrensmeyer and Hook 1992). Aeolian vertebrate-bearing deposits are relatively uncommon throughout the record but still provide rare examples of spectacular preservation and unusual windows into past ecosystems (e.g. the Mesozoic aeolian deposits of the Gobi Desert in Mongolia; Behrensmeyer and Hook 1992). Skeletal concentrations in archaeological sites occur only in latest Pliocene to Recent time and represent a new type of carcass-processing and bone-collecting behaviour associated with human evolution.

Environmental biases in the vertebrate fossil record

The Phanerozoic record of land vertebrate palaeobiology is derived primarily from fluvial, deltaic, and lacustrine environments; species and body plans that may have existed in other environments are poorly represented until the Cenozoic. Thus, there is an overall bias in favour of animals that inhabited moist, lowland riverine, and lake margin habitats, and such habitats may have been relatively homogeneous compared with topographically diverse 'uplands'. Fossils from channel lags and bars in lowland riverine settings can reflect species diversity in a fluvial system as a whole, but sampling of a range of fluvial subenvironments provides more reliable representation of diversity as well as information on finer-scale patterns of species distribution and abundance.

The environmental imprint on the faunal composition of fossil assemblages is strong enough for faunas from the same type of deposit (e.g. abandoned channels) to be more similar through time than faunas from different taphonomic settings of the same age (e.g. fissure fills vs. abandoned channels). This can lead to problems in ordering faunas biostratigraphically or documenting diversity fluctuations through time, and it is important to control for palaeoenvironmental context, time-averaging, and other taphonomic biases when faunal lists from a wide range of localities are used for such purposes.

References

Andrews, P. (1990) *Owls, caves and fossils*. Natural History Museum, London.

Badgley, C.E. and Behrensmeyer, A.K. (1995) Long records of continental ecosystems. *Palaeogeography, Palaeoclimatology, Palaeoecology* **115**, Special issue (Nos. 1–4).

Behrensmeyer, A.K. (1991) Terrestrial vertebrate accumulations. In: P.A. Allison and D.E.G. Briggs, eds. *Taphonomy: releasing the data locked in the fossil record*, pp. 291–335. Plenum, New York.

Behrensmeyer, A.K. and Hook, R.W. (1992) Paleoenvironmental contexts and taphonomic modes in the terrestrial fossil record. In: A.K. Behrensmeyer, J.D. Damuth, W.A. DiMichele, R. Potts, H.-D. Sues and S.L. Wing, eds. *Terrestrial ecosystems through time*, pp. 15–136. University of Chicago Press, Chicago.

Graham, R.W. (1993) Processes of time-averaging in the terrestrial vertebrate record. In: S.M. Kidwell and A.K. Behrensmeyer, eds. *Taphonomic approaches to time resolution in fossil assemblages*, pp. 102–124. Short Courses in Paleontology, no. 6. The Paleontological Society, Knoxville, Tennessee.

Smith, R.M.H. (1993) Vertebrate taphonomy of Late Permian floodplain deposits in the southwestern Karoo Basin of South Africa. *Palaios* **8**, 45–67.

3.3.8 *Sphagnum*-dominated Peat Bogs

T.J. PAINTER

Introduction

Sphagnum-dominated peat bogs are important as havens for wildlife but, until they are drained, they have little practical value except as garbage dumps. They are also treacherous, because *Sphagnum* mosses can grow over the surfaces of deep pools, creating the illusion of solid terrain. Hence domestic refuse and the remains of unwary animals are prominent among the many items that can be found preserved in *Sphagnum* peat. The bodies of executed criminals and murder victims, especially those sacrificed ritually by the Druids (300 BC to AD 100), were routinely deposited in peat bogs (Fig. 3.3.8.1). Less sensational but equally fascinating are the leaves of dicotyledons, thousands of years old, that normally would have decayed rapidly. Whole villages built of wood and wattle, up to 6000 years old, including unconsumed bread, cereal grains, nuts, fruits and berries, and even the excreta of domestic animals, have also been found buried in *Sphagnum* peat (Coles and Coles 1989).

The preservative properties of this kind of peat were apparently known to ancient peoples, because hundreds of wooden butter kegs, some containing butter up to 1800 years old, have been discovered in subterranean larders, excavated in Irish and Scottish peat bogs. For many centuries, Scandinavian anglers have submerged their 'catches' in undrained peat bogs as a means of keeping the fish 'fresh' until they were ready to consume

Fig. 3.3.8.1 Tollund Man, about 2200 years old, was found near Silkeborg, Jutland, Denmark, in May 1950. The melanoid skin pigmentation is the result of a Maillard reaction between the skin proteins and sphagnan. (Courtesy of the Silkeborg Museum, Denmark.)

it. It should, however, be noted that peats derived exclusively from sedges are not known to preserve biological materials other than the sedges themselves. Sedges contain silica, and their resistance to decay under acidic conditions probably arises because the silica provides a physical barrier to microbial attack (Painter 1995).

Sphagnum mosses as scavengers of atmospheric nutrients

Survival 'strategy'

Sphagnum mosses (Fig. 3.3.8.2a) specialize in growth under conditions of extreme nutrient limitation. This effectively eliminates competition from all but a few vascular plants, such as sedges (especially *Eriophorum* spp.) and heath plants (notably *Calluna* and *Vaccinium*). Like other bryophytes, *Sphagnum* mosses have no roots, and they absorb dissolved nutrients from the ambient water directly through their leaves; but they surpass the others in the extraordinary efficiency with which they do this. In the early stages of bog formation, they float on water that has collected in basins in impervious rocks, and which typically has a very low content of nutrients or other solutes. After they have filled the basins and grown above the influence of ground water, they extract their nutrients mostly from rainwater, in which the concentration of solutes is again very low. The unique extraction process explains the biological success of the genus; it is also the key to an understanding of the preservation phenomenon (Clymo and Hayward 1982; Painter 1998).

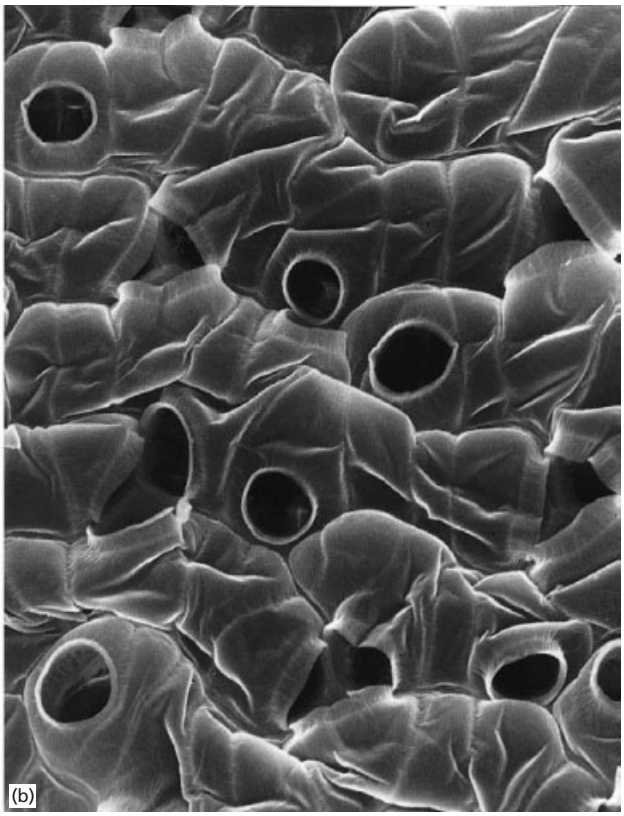


Fig. 3.3.8.2 (a) *Sphagnum palustre* is a prominent peat-producer in coastal and other lowland regions of northern Europe today; it is a close relative of *S. imbricatum*, the species mainly responsible for the preservation of Lindow Man (about 2000 years old, found in Cheshire, England, in 1984); the compound leaves are ≈ 6 mm long. (b) Scanning electron micrograph of a leaf of *S. palustre*; the average diameter of the circular openings ('pores') is 13 μm; as rainwater flows under gravity through the tubes formed by these empty, hyaline cells, it passes over the surfaces of the smaller, chlorophyllose cells which absorb the traces of ammonia and nutrient salts that it has washed out from the atmosphere. (a, Photograph by K.I. Flatberg.)

The apparatus of extraction

About 90% of the volume of a *Sphagnum* leaf is made up of long, empty, thin-walled ('hyaline') cells with circular or elliptical openings ('pores') through which rainwater enters and leaves under gravity (Fig. 3.3.8.2b). The water passes through tubes supported on the inside by hoops with transverse struts. The walls between the hoops are flexible, which permits them to expand or contract in proportion to the water supply. The diameter of the pores on the concave surfaces of the leaves (which entrap droplets of rainwater) is such that the surface tension prevents the cells from discharging their water until more is supplied. The living, chlorophyllose cells nestle in between the hyaline cells, absorbing dissolved nutrients from the rainwater flowing through them (Clymo and Hayward 1982).

Uptake and storage of nitrogen

The nitrogen extracted from rainwater is mainly in the form of ammonia washed out from the atmosphere, but in dry weather gaseous ammonia can be absorbed directly from the atmosphere by the water in the leaves. The ammonia normally originates mainly from the decay of organic matter and forest fires outside the bog area (Painter 1998).

In the roots of vascular plants, ammonia taken up by the living cells is first incorporated into glutamine (Gln), which serves as a 'carrier' of ammonia for use in other reactions, including especially the replacement of keto groups by amino groups. For example, α-keto-glutaric acid (KG) is converted into glutamic acid (Glu) (Fig. 3.3.8.3) (Woodall *et al.* 1996). The α-keto-carboxylic acid group ($-CO-CO_2H$) has a strong affinity for ammonia and primary amines of all kinds, and will condense readily with them, even without the help of an enzyme. It should, however, be noted that all these metabolites are soluble in water, and all of the reactions mentioned so far occur in the cytoplasm of living cells. They could not occur in the empty hyaline cells unless the α-keto-carboxylic acid groups were

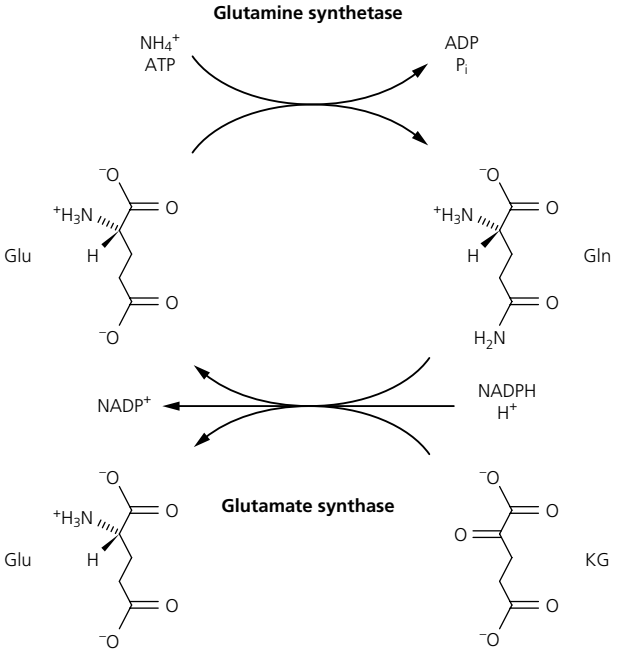


Fig. 3.3.8.3 The principal pathway of ammonium assimilation in living plant cells. With the help of energy provided by the hydrolysis of ATP, glutamine synthetase adds ammonium ions to glutamate (Glu) to give glutamine (Gln). Glutamate synthase then uses Gln and NADPH to aminate α-keto-glutarate (KG), giving glutamate (Glu). Glutamate can then pass on its amino group to many other α-keto-carboxylic acids, giving amino acids of all kinds (Woodall *et al*. 1996).

somehow immobilized on the surfaces of the hyaline cell walls.

This reasoning introduces the discovery of 'sphagnan'. It is an acidic polysaccharide that resembles the complex pectins of higher plants but, in addition to residues of galacturonic acid and neutral sugars, it contains side-chains with residues of D-*lyxo*-5-hexosulouronic acid. This sugar is trivially named as 5-keto-D-mannuronic acid, abbreviated to 5KMA. The reactive α-keto-carboxylic acid groups occur in the furanose form, which is interconvertible with the pyranose form (Fig. 3.3.8.4). Sphagnan comprises about 55% of the 'holo-cellulose' (the total cell-wall polysaccharides in the moss). Besides serving as a trap and storage depot for ammonia, its 5KMA residues are responsible for cross-linking between pectinous, cellulosic, and hemicellulosic (xyloglucomannan) chains (Painter 1995, 1998). It should be emphasized that sphagnan's affinity for ammonia, though strong, is non-selective. It also binds other primary amines, including amino acids, proteins, and enzymes of all kinds; and this property is the essence of the preservation phenomenon.

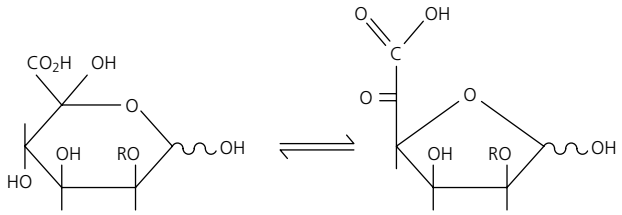


Fig. 3.3.8.4 Structure of 5-keto-D-mannuronic acid (5KMA) in its six-membered (pyranose) ring form (left) and its highly reactive, five-membered (furanose) ring form (right). The two isomeric ring structures are interconvertible under mildly acidic conditions. The letter R signifies the point of attachment of a polysaccharide (xyloglucomannan) side-chain.

Uptake and storage of essential metal cations

The nutrient salts in rainwater originate mainly from the oceans and deserts, from which droplets of sea water or dust particles are easily swept up by strong winds and transported over long distances in the upper atmosphere. Living *Sphagnum* mosses have an impressive cation-exchange capacity. This is due almost entirely to the sphagnan in the hyaline cell walls. The anionic groups are supplied by residues of D-galacturonic acid and 5KMA, which jointly represent ≈50% of the sphagnan molecule (≈25% each). Sphagnan binds multivalent metal cations with high selectivity, and hence the extraction of those that are essential for growth is highly efficient (Clymo and Hayward 1982; Painter 1995).

Diagenesis

Spontaneous release of soluble sphagnan

The cross-linkages that the 5KMA residues in sphagnan form with the other polysaccharide chains in the living moss are extremely sensitive to acids, and under the mildly acidic conditions in the bog they hydrolyse spontaneously. This autocatalytic reaction releases soluble sphagnan very slowly into the bog water over a period of 2000 years or more. At the same time, the hyaline cell walls lose their distinctive morphology and porosity, and are converted into a relatively dense, amorphous solid—pasty when wet but hard and brittle like clay when dry (Painter 1995, 1998).

Spontaneous humification: the Maillard reaction

Both before and after cleavage of all the cross-linkages (that is, in both the bound and soluble forms of sphagnan), the 5KMA residues spontaneously lose the elements of water and carbon dioxide and are thereby converted into a polymer with a partly aromatic, dark-brown chromophore as well as unmodified carbohyd-

rate. This process may be compared with caramelization, but it goes faster because ketouronic acids are fundamentally less stable than ordinary sugars. When ammonia or any other primary amine (including amino acids, proteins, and enzymes) is present, the reaction goes even faster and nitrogen becomes irreversibly incorporated by covalent chemical linkages into the structure of the chromophore. This special kind of 'caramelization' that occurs in the presence of amines is known as a 'Maillard reaction' and the dark brown, polymeric end-product is called a 'melanoidin'. Melanoidins contain both anionic and cationic groups, and are powerful chelating agents. Their affinities for many multivalent metal cations greatly exceed those of the reducing sugars and amino acids from which they are commonly formed; and this is also true of peat humic acids compared with unmodified sphagnan (Painter 1998).

Mechanisms of preservation

Sequestration of amino-nitrogen and essential multivalent metal cations

Rainfall over northern Europe usually contains <100 µmol/l (1.7 ppm) of dissolved ammonia, and after filtration through a carpet of living *Sphagnum*, virtually none would remain. Similar considerations apply to the multivalent metal cations that are essential for microbial growth. This explains why the density of bacterial cells in the anoxic region of a peat bog (below about 40 cm from the surface) is, on average, about one-millionth of that in a heap of rotting grass; but not why the bacteria have such difficulty in digesting the dead moss and other tissues, so as to release these nutrients.

Deactivation of digestive enzymes secreted by saprogenic microorganisms

Laboratory experiments have shown that digestive enzymes of all kinds, including microbial proteases, cellulases, amylases, and pectinases, are irreversibly bound and deactivated by *Sphagnum* holocellulose. Some lose their activity completely within a few hours, but the activity of most decay with a half-life of 1–2 days (Painter 1995). This points to a generalization of critical significance: direct involvement of an enzyme in a Maillard reaction usually destroys its activity.

Tanning of collagen and other proteins by sphagnan

The soluble form of sphagnan reacts also with insoluble, fibrous proteins, including collagen and keratin. Animal skins immersed in sphagnan solutions rapidly acquire the characteristic, brown pigmentation of the Maillard melanoidins; after several weeks they are, essentially, leather. This tanning reaction involves the cross-linking of collagen fibres by the numerous α-keto-carboxylic acid groups that are distributed over the surfaces of the polymeric sphagnan molecules (Painter 1995).

Conclusion

Sphagnan promotes preservation by sequestering ammonia and essential metal cations, neutralizing digestive enzymes, and tanning fibrous proteins. All four factors combine to prevent the efficient functioning of decay organisms.

References

Clymo, R.S. and Hayward, P.M. (1982) The ecology of *Sphagnum*. In: A.J.E. Smith, ed. *Bryophyte ecology*, pp. 229–289. Chapman and Hall, London.

Coles, B. and Coles, J. (1989) *People of the wetlands*: *bogs, bodies and lake-dwellers*. Guild Publishing, London.

Painter, T.J. (1995) Chemical and microbiological aspects of the preservation process in *Sphagnum* peat. In: R.C. Turner and R.G. Scaife, eds. *Bog bodies: new discoveries and new perspectives*, pp. 88–99. British Museum Press, London.

Painter, T.J. (1998) An integrated view of the Maillard reaction, with special reference to discoveries of preserved food in *Sphagnum*-dominated peat bogs. *Carbohydrate Polymers* **36**, 335–347.

Woodall, J., Boxall, J.G., Forde, B.G. and Pearson, J. (1996) Changing perspectives in plant nitrogen metabolism: the central role of glutamine synthetase. *Science Progress* **79**, 1–26.

3.3.9 Archaeological Remains

V. STRAKER

Introduction

A wide range of biological remains can be preserved in the deposits that comprise, underlie, or bury archaeological sites, and in the landscapes around them (Table 3.3.9.1). Sufficient is known about the ecological affinities and associations of many plant and animal species to allow inferences to be made regarding former environments, using uniformitarian reasoning (Bell and Walker 1992); however, specialists also use experimental results and ethnographic observations to interpret their data.

The science of environmental archaeology, broadly defined as the study of the ecology of past human communities, and the history of the relationships between

Table 3.3.9.1 The biological remains most commonly studied in archaeological projects.

Plant	Phytoliths	Mosses
	Diatoms	Fruits, seeds, buds, leaves, etc.
	Pollen and spores	Wood and charcoal
	Fungal spores	
Animal	Ova of mammalian internal parasites (especially nematodes)	Insects and arachnids (exoskeletons, especially of beetles and mites)
	Foraminifera (tests)	Molluscs (shells)
	Cladocera and ostracods (valves and egg cases)	Large crustaceans (e.g. crab claws)
	Chironomids (larval head capsules)	Vertebrates (bones and teeth)

people and environments, has developed as a mainstream subdiscipline of archaeology in the last 30 years. It is a multidisciplinary subject that draws upon the techniques and methodologies of the biological and Earth sciences and can be divided broadly into bioarchaeology and geoarchaeology. As it is concerned with reconstructing former environments, the scope of environmental archaeology overlaps to a considerable extent with Quaternary palaeoecology.

Biological remains surviving in 'on-site' settlement contexts (e.g. floor layers, rubbish pits, hearths, ditches, post holes) illuminate topics such as the economic basis for early societies and the nature of their dwellings and living conditions, trade in non-indigenous plants and animals and their introduction to new areas, and the uses of plants and animals for industrial purposes. Buried soils (also known as old land surfaces) preserved under earthworks, for example, can reveal the nature of the preburial environment. Burial contexts, whether inhumations or cremations, contribute data on past populations, their health, and their burial practices.

The 'off-site' evidence provides a vital temporal and environmental context from which to view the site-based data. This is collected from a wide range of deposits, including mires, palaeochannels, alluvial sequences, lake, intertidal, and cave sediments, and palaeosols.

As well as analysis of the biological data, the sediments in which they are preserved can be subjected to a range of geochemical, pedological, and sedimentological techniques to determine their origin and past climatic and environmental conditions.

Preservation in different environmental settings

The term 'subfossil' is often applied to archaeological remains where chemical composition is unchanged from that in life (Evans 1978), apart from the processes of decay resulting in, for example, loss of cell contents. Archaeological assemblages rarely, if ever, present a complete picture of the biological material that was originally buried, since they are affected by taphonomic processes (Bell and Walker 1992; Evans and O'Connor 1999). A large range of factors involved, including conditions of burial and postdepositional disturbance (such as predation by living organisms or the addition of organisms not originally present in the death assemblage). A further major consideration is that, given the variability of the chemical composition of biological organisms, their preservation potential under different environmental conditions varies.

Charring

The remains of fruits, seeds, and wood usually only survive if charred (see also Section 3.2.3), unless preserved in deposits that have been constantly waterlogged since (or shortly after) deposition, or in desiccating conditions in deserts. Where conditions are generally dry but non-desiccating, the recovery of macroscopic plant remains is biased towards charred remains, mainly of arable crops and associated wild species, which were accidentally burnt during crop processing or cooking. The burning down of a dwelling or food store also results in charred preservation.

Mineral replacement

Mineralized fruits, seeds, roots, and invertebrate remains such as earthworm cocoons and millipedes have been recovered from archaeological sites in Britain, from the late Bronze Age (notably at Potterne in Wiltshire) onwards. Rapid burial, rapid decay of soft tissues, and partially (but not fully) waterlogged conditions, may all play a part in the replacement of plant and animal tissues by calcium carbonate or calcium phosphate. These remains are of importance to the archaeologist because, on dry sites, they complement the partial record provided by charred plant macrofossils.

Silicification

Occasionally, macroscopic skeletons of silica-rich parts of plants that do not normally survive the charring process, such as the upper parts of cereal glumes, paleas, and lemmas, are recovered. These appear to survive because high temperature oxidizing conditions burn out all the carbon, leaving only the silica skeleton, preserved perhaps because metal salts (present in small amounts in plant cells) react with the phytolith surfaces to form glass with a lower melting point than silica, welding the phytoliths together.

Waterlogging

Anaerobic environments, such as the drowned remains of the prehistoric lake villages of Switzerland and southern Germany, preserve uncharred plant and animal remains which often appear, at least to the naked eye, to be in excellent condition. However, examination of waterlogged wood or other plant material under a high-power microscope usually reveals fungal hyphae and spores, and other agents of decay. Arthropod remains such as insects can be recovered from waterlogged sediments, but do not survive in dry soils. Excavation of deep stratigraphy in towns such as London, York, and Dublin has shown that preservation of uncharred organic material can be excellent, despite the fact that the sediments are not actually waterlogged, but simply deeply buried and largely anoxic.

Acidity and alkalinity

Another major factor influencing preservation is the acidity or alkalinity of the burial environment. Bones, mollusc shells, and ostracods, for example, usually do not survive in acid soils or acid peat bogs. Here microbial activity may be prevented or slowed down, enhancing preservation of non-biomineralized material. Pollen survives well in acid bogs and soils, but poorly in oxic soils such as rendzinas on chalk where soil microbes are active. In this case, differential preservation often occurs; the relatively robust pollen of hazel and spores of ferns, for example, may survive better than the rest of the original assemblage.

Desiccation

In dry deserts both plant and animal remains are remarkably well preserved by desiccation and resemble, at least superficially, their modern equivalents. At the multiperiod site of Qasr Ibrim in the Nile valley, for example, desiccated preservation of uncharred plants is spectacular, and animal skeletons may remain partly articulated with the survival of tendons, fur, and skin.

Freezing

Preservation is also excellent in frozen conditions as demonstrated by the body of the 'Iceman', found in the South Tyrol in 1991. The bones, teeth, internal organs, and skin (retaining details of tattoos) of a late neolithic man were preserved, as well as clothes made of fur and plaited grasses, and his possessions. These included a bow made of yew, two birch-bark containers, a quiver of arrows, and many other personal items (Spindler 1994).

Although preservation of biological remains is enhanced where microbial activity is reduced (e.g. by acidity, extreme cold or dryness, or anoxic conditions), there are many other complex and interacting factors which affect it. Pollen grains and insect exoskeletons are not always well preserved in waterlogged peat bogs, for instance, and one factor that may be important is whether the bog is, or has been, affected by oxygen- or nutrient-enriched water where microorganisms are active.

Experimental earthworks

Little experimental work has been done on the effects of burial on organic material in an archaeological context. The main contribution has been from the Experimental Earthworks Project. In 1960 an earthwork was constructed on chalk at Overton Down, Wiltshire, and in 1963 another was built on acid sands at Mordon Bog, Dorset (both UK). The objective of the project was to study the short- and medium-term changes that an earthwork and its contents undergo, in order to better understand the formation of the archaeological record.

Textiles (cotton, wool, gabardine, and linen), leathers and goatskin, hemp and flax ropes, charred and uncharred oak and hazel wood, and cooked, uncooked, and cremated bone were buried on the soil surface beneath the turf stacks which formed the central core of the banks, beneath the banks but away from the turf core, and within the banks. Sections through the earthwork were to be excavated at 2, 4, 8, 16, 32, 64, and 128-year intervals and the buried materials examined. Bell *et al.* (1996) published a range of analyses carried out after 32 years of burial at Overton Down, including some techniques for studying the degradation of biological material not foreseen in 1960 (such as scanning electron microscopy and DNA analyses of bone, and microbiological analyses of the burial environment and buried wood and leather). The preservation of organics was much poorer in the turf than in the chalk environment. Leathers survived very well in both environments, whereas wool and linen were very degraded even in the chalk. Uncharred wood only survived in the chalk, and hazel had resisted soft rot fungi better than oak.

Scanning electron microscopy revealed postburial modification of bone, particularly in the turf environment.

References

Bell, M. and Walker, M.J.C. (1992) *Late Quaternary environmental change*. Longman Scientific and Technical, Essex; John Wiley, New York.

Bell, M., Fowler, P.J. and Hillson, S.W. (1996) *The Experimental Earthwork Project 1960–92*. Council for British Archaeology Research Report No. 100, York.

Evans, J.G. (1978) *An introduction to environmental archaeology*. Elek, London.

Evans, J.G. and O'Connor, T. (1999) *Environmental archaeology: principles and methods*. Sutton Publishing, Stroud, Gloucestershire.

Spindler, K. (1994) *The man in the ice*. Weidenfeld and Nicolson, London.

3.4 Lagerstätten

3.4.1 Exceptionally Preserved Fossils

D.E.G. BRIGGS

Introduction

Extraordinary fossil occurrences are commonly referred to as Fossil-Lagerstätten (see Seilacher *et al*. 1985). Two types of Fossil-Lagerstätten are normally recognized: (1) concentration deposits, where the occurrence is remarkable for the sheer abundance of specimens (e.g. bone beds, coquinas); and (2) conservation deposits, where the preservation is of unusual quality (e.g. articulated skeletons, fossilized soft tissues). Concentration deposits (Konzentrat-Lagerstätten) typically accumulate over a significant period of time and the fossils have therefore been subjected to time-averaging (see Section 3.2.7). Conservation deposits (Konservat-Lagerstätten), on the other hand, are usually the result of a catastrophic event, such as rapid burial, and represent an instant in geological time. Conservation deposits have attracted more attention because of their higher information content, particularly those that preserve the non-biomineralized (so-called 'soft') tissues of organisms, which are the focus here. Their major importance to the study of the history of life lies in the much more complete picture of ancient communities that they afford, compared to the normal fossil record of hard skeletons.

The context and style of preservation of soft-bodied fossils is determined by a hierarchy of controls. Although these controls are not yet fully understood, they help to explain why exceptional preservation is confined to certain settings, and what processes lead to the fossilization of soft tissues. Furthermore, research on the taphonomy of soft-bodied fossils is of wider significance; such specimens provide evidence of the impact of microbial activity in sediments on the decay and preservation of organic matter, and the formation of authigenic minerals.

The history of life and the distribution of the continents

Konservat-Lagerstätten are abundant in particular settings during different intervals of geological time. The distribution of these 'taphonomic windows' is controlled largely by major events in the evolution of life, and by the distribution of the continents (Allison and Briggs 1991, 1993).

Prior to the appearance of biomineralized skeletons in the late Precambrian and Early Cambrian (see Section 1.2.2), special conditions were required for preservation. The widespread occurrence of Ediacaran fossils in shallow marine settings reflects the absence of grazing invertebrates, and the resultant prevalence of microbial mats (matgrounds: Seilacher 1999). The diversification of invertebrates in the Cambrian ensured that microbial mats were no longer ubiquitous, and the preservation of soft tissues required other special circumstances. The Burgess Shale-type Lagerstätten of the Cambrian are most abundant in deeper slope/basin settings, where fine-grained sediment accumulated in episodic depositional events. At this time deep bioturbators had yet to invade deeper water settings in large numbers; their subsequent radiation from onshore to offshore contributed to the absence of Burgess Shale-type Lagerstätten in younger rocks (Allison and Briggs 1993).

The Carboniferous was characterized by wide areas of broad coastal delta plains in tropical latitudes. In this setting, transitional from terrestrial to marine, interdistributary bays and lagoons favour episodic sedimentation, high organic input, and fluctuating salinity. Mazon Creek-type biotas are frequent in such settings in the Carboniferous, but also occur in the Triassic (Grès-à-Voltzia, France). They preserve a wealth of animal and plant fossils, reflecting the complexity of terrestrial and nearshore marine habitats.

Shallow restricted marine basins in tropical, semiarid regions result in a stratified water body; the low oxygen and high salinity conditions favour the growth of microbial mats (see Section 3.2.4). The bedded limestones (plattenkalks) which are deposited in such settings were most widespread during the Mesozoic (particularly Jurassic), but yield examples of Solnhofen-type exceptional preservation from the Carboniferous to the Tertiary.

Lake settings are vulnerable to erosion and destruction by tectonic activity and the majority of lacustrine sequences are Tertiary in age. Their laminated sediments yield exceptionally preserved plants, insects, fishes, and even birds and tetrapods. Earlier examples, such as the Cretaceous of Las Hoyas, Spain (see Section 3.4.9), are rarer and therefore particularly important.

The preservation of fossils in resin depends on the appearance of resin-producing plants. The oldest fossil resins are Carboniferous, the product of pteridosperms. The oldest inclusions in amber are Triassic spores and microorganisms; insects are known from amber as old as Cretaceous. The most diverse and abundant amber assemblages are Tertiary, mainly from *Hymenaea* trees (see Section 3.4.11).

Environment of deposition

The settings in which Konservat-Lagerstätten are preserved extend from offshore marine (the Cambrian Burgess Shale), through shallow water (most Ediacaran biotas), to restricted marine basins (the Jurassic Solnhofen Limestone); non-marine organisms are represented in lake deposits, and may be trapped in amber.

The major environmental controls on the formation of conservation deposits are those which eliminate scavengers: anoxia (stagnation) and rapid burial (obrution) (Seilacher *et al.* 1985). Exceptional preservation is favoured by anoxic bottom conditions and large episodic influxes of sediment. The organisms that become fossilized are often transported to an environment which is unfavourable to life (e.g. Burgess Shale, Solnhofen Limestone). In some cases, however, a fauna may be overwhelmed *in situ*, and anoxic conditions established as a result of initial decay (e.g. Hunsrück Slate). Scavengers can also be excluded by other factors, such as elevated salinity. In those settings microbial mats may be an important agent in promoting preservation (see Section 3.2.4). They function by stabilizing the sediment and by setting up geochemical gradients which promote early mineralization. Preservation in hot siliceous springs (see Section 3.4.5), amber (see Section 3.4.11), and peat (see Section 3.3.8) involves very specific environmental controls, and can be categorized as conservation traps (Seilacher *et al*. 1985).

Sediment chemistry

Non-biomineralized tissues display a spectrum of resistance to decay (see Section 3.2.1). At one end are robust structural tissues, such as arthropod cuticles and the seed coats and woody tissues of plants, which are decay resistant and may be incorporated into the fossil record as organic remains. At the other end are decay-prone tissues, such as muscle or gut, which degrade very rapidly; they are only preserved when they are replicated very rapidly in authigenic minerals. Both organic and inorganic preservation may occur in the same deposit, or even in the same fossil.

The formation of authigenic minerals is controlled by the chemistry of the carcass and the surrounding sediment, including the development of geochemical gradients during decay, and the concentrations of mineral-forming ions. A number of minerals may precipitate around a decaying carcass to form a concretion, or replicate the morphology of the organism by precipitating on or within the tissues. Microbial decay is necessary to generate the conditions required for mineralization and, in some cases, to release the ions that form the minerals. The setting required for this type of preservation can be inferred from fossil examples, but only experiments can provide information on conditions and length of time required for replication. Experiments show that steep chemical gradients form around a decaying carcass prior to mineralization, which occurs within weeks or months.

Apatite

The mineral that most commonly preserves soft tissues is apatite (see Section 3.4.8). Its formation requires a sufficient concentration of phosphate (released from decaying carcasses and accumulated in the surrounding sediment), and specific pH and redox conditions. Apatite precipitates very rapidly as tiny crystallites (often <30 nm) and preserves morphological detail of the highest fidelity, even subcellular in some circumstances. The detail that survives depends on whether the microbes that drive mineralization themselves become mineralized (Wilby and Briggs 1997). Two main textures can be recognized: (1) *microbial* (Fig. 3.4.1.1a), where

tissues are preserved through mineralization of the infesting microbes (in such cases the fidelity of replication is limited by the size of the microbes); and (2) *substrate* (Fig. 3.4.1.1b), where the tissues themselves are phosphatized by amorphous crystallites, microbes are not mineralized, and much higher fidelity is the result. A third, *intermediate* mode of preservation involves phosphatization of the tissue, but retention of moulds of the former position of microbes. All three types of phosphatization may occur in fossils from the same Konservat-Lagerstätte, or even within the same fossil. The distribution of textures is, to some degree, taxon controlled—arthropods tend to be dominated by microbial microfabrics, cephalopods by microbial and substrate, and fish by substrate. This reflects the degree to which microbes can penetrate different types of carcass (Wilby and Briggs 1997).

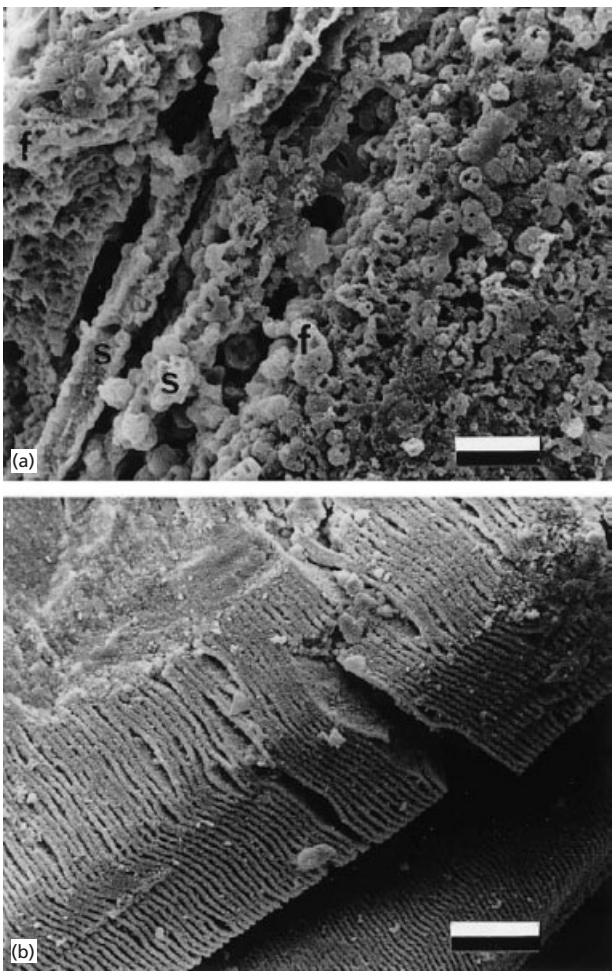


Fig. 3.4.1.1 Preservational styles in apatite. (a) Microbial microfabric in muscle fibres from a fish from Monte Bolca (Eocene, northern Italy); the fibres, which run NE–SW, are completely pseudomorphed by phosphatized bacteria, many of which are preserved as hollow spheres; the sarcolemma (s) or sheath can be distinguished from the fibres (f) that it surrounds; scale 4 µm. (b) Substrate microfabric in muscle tissue from the ray *Squatina alifera* from the Solnhofen Limestone (Jurassic, Germany); banding is clearly evident due to separation of the sarcomeres during rigor mortis accentuated by decay; scale 20 µm. (After Wilby and Briggs 1997.)

Clay minerals

Clay minerals can replicate soft tissues with a similar fidelity to apatite, in conditions of low pH. Muscle fibres are replicated in clay minerals in the giant conodont animal *Promissum pulchrum*, arthropods, and other taxa from the Ordovician Soom Shale (see Section 3.4.4). Clays may also coat decay-resistant organic remains, like the eye capsules of conodonts. Clay minerals played a fundamental role in the preservation of fossils of the Cambrian Burgess Shale, which involved a combination of organic preservation and authigenic mineralization. Organic structures, like the sclerites of *Wiwaxia* or the setae of polychaetes, have been altered to a kerogen- or graphite-like substance, and can be isolated from the rock matrix using hydrofluoric acid. However, associated with this carbon are clay minerals which precipitated on the surface of these and less decay-resistant tissues (Orr *et al.* 1998). Elemental mapping (Fig. 3.4.1.2) reveals that different clay minerals have formed on different tissues. This selectivity may reflect the chemical composition of the tissues themselves, or their susceptibility to decay; such a mode of preservation is unlikely to be unique to Burgess Shale-type faunas.

Pyrite

The preservation of soft tissues in a clay-rich sediment does not always involve the precipitation of clay minerals in association with the carcass. In rare cases, where the concentration of iron is high, and organic material is confined mainly to isolated carcasses or plant remains, soft tissues may be preserved in pyrite. The best-known case is the Devonian Hunsrück Slate of western Germany (see Section 3.4.6), but there are numerous examples of pyritized plant material. Organic matter provides a locus for precipitation, but the process is slower than the formation of apatite or clay minerals. In arthropods pyrite precipitates within the exoskeleton while most of the internal structures, such as muscle, decay. The limbs are preserved as a pyrite fill. Cellular details may survive in plants; pyrite infills the cell lumina in plants from the Eocene London Clay. The organic material may subsequently decay, or some of it may remain, particularly in the case of plant fossils.

Other minerals

A variety of other minerals are important in soft-tissue

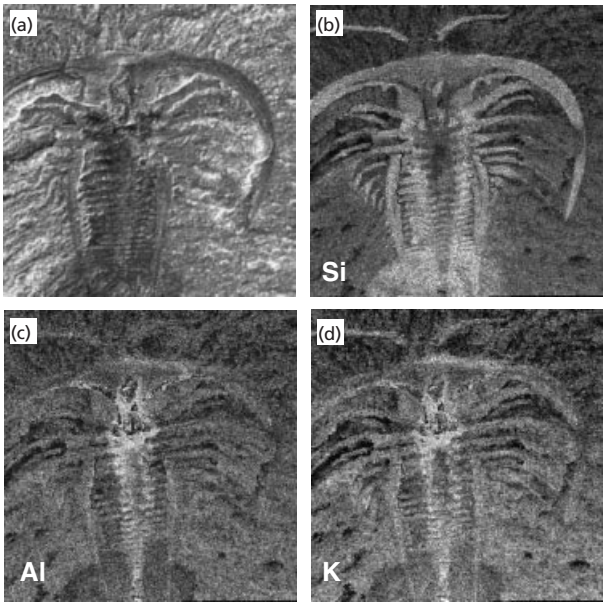


Fig. 3.4.1.2 Mineralization of the arthropod *Marrella splendens* from the Cambrian Burgess Shale, ×2.65. (a) Under incident light. (b–d) Elemental maps for Si, Al, and K; the brighter the tone the more abundant the element; note that the cuticle is characterized by elevated Si, and the stomach (in the centre of the headshield) and axis of the trunk by Al and K, reflecting different clay mineral compositions. (After Orr *et al.* 1998.)

preservation, notably silica (particularly in Precambrian microbiotas) (see Section 3.4.2) and calcite. The extraordinary three-dimensional fossils from the Jurassic of La Voulte-sur-Rhône were apparently preserved in a setting with a high concentration of metal sulphides (see Section 3.4.7). They reveal a diagenetic sequence which shows that rapid mineralization in apatite preserved morphological details which were subsequently transformed into other minerals, including calcite, pyrite, and galena. In a number of Konservat-Lagerstätten (e.g. the Santana Formation: see Section 3.4.8) the formation of concretions around the fossils played a critical role in their preservation and subsequent protection from compaction.

Tissue type/composition

The most decay-prone tissues require mineralization to preserve their morphology and are therefore only preserved where the requisite conditions prevail (see Section 3.2.1). More decay-resistant organic structures, however, may survive to be incorporated in the sedimentary record (Briggs 1999). A range of biopolymers make up organisms: nucleic acids (DNA, RNA), proteins, polysaccharides, lipids, as well as the biomacromolecules that form structural tissues in both plants and animals. DNA is highly susceptible to hydrolysis and oxidation, and there are no reliable traces in fossils much more than 50 000 years old (see Section 3.1.1). Proteins also decay rapidly and are usually only preserved on a time scale similar to that for DNA (see Section 3.1.2). Polysaccharides, such as cellulose and chitin, are readily broken down, except where they are cross-linked with other molecules to form structural tissues (see Section 3.1.6). The most widely studied fossil biomolecules are lipids, which alter to form biomarkers diagnostic of a variety of environmental parameters (see Section 3.1.3). The components of soft-bodied fossils that survive as organic remains, however, are generally structural tissues—toughened to serve for support and protection in life, the cross-linking makes them more decay resistant (see Sections 3.1.5 and 3.1.6). Thus the composition of these tissues controls whether or not they are selectively preserved. Through time, however, they may be transformed, by *in situ* polymerization, into even more decay-resistant hydrocarbons (aliphatic or aromatic in composition). This process destroys the microstructure and layering of the tissue, but preserves its external appearance (see Briggs 1999).

Fossilization is a long-term process, but the factors that determine whether or not soft tissues are preserved operate on a laboratory time scale. Even the most completely preserved organisms have undergone some decay; microbial activity is necessary to establish the conditions that lead to the formation of authigenic minerals. Experiments can reveal the sequence in which tissues decay, and provide a more realistic basis for interpreting soft-bodied fossils than freshly killed modern organisms. Decay experiments on the lancelet *Branchiostoma*, for example, allowed features of conodont animal specimens to be interpreted, including the identity of the notochord and the discrete nature of the V-shaped muscle blocks (Briggs 1995). The sequence in which tissues of particular type and composition decay provides a scale against which the quality or completeness of preservation in a Konservat-Lagerstätte can be measured. The recognition of such taphonomic thresholds can reveal biases in fossil assemblages—if the soft tissues of polychaete worms are preserved, for example, the absence of other soft-bodied taxa may be real, rather than simply a function of their low preservation potential.

Conclusion

The focus on controls on exceptional preservation has narrowed from regional to sedimentological, and from geological setting to process, to the level of the organism. Soft-tissue fossilization relies on the microbial processes that cause decay and drive mineralization. Labile tissues are only preserved where authigenic mineralization occurs. Macromolecular material may be selectively pre-

served, but the long-term preservation of organic macrofossils involves diagenetic alteration.

Konservat-Lagerstätten, by their very nature, provide data far beyond that available in the shelly fossil record. This information has proved fundamental to our understanding of the evolution and phylogeny of almost all animal and plant groups. However, because of the scattered distribution of conservation deposits, there are difficulties in incorporating the data into analyses of fluctuations in diversity through time. Understanding the controls on exceptional preservation will guide the search for new examples. It will also help in reconciling data from the shelly fossil record, which is more continuous but less representative of diversity as a whole, with those from the record of Konservat-Lagerstätten, which document diversity intermittently but more completely.

References

Allison, P.A. and Briggs, D.E.G. (1991) Taphonomy of nonmineralized tissues. In: P.A. Allison and D.E.G. Briggs, eds. *Taphonomy: releasing the data locked in the fossil record*, pp. 25–70. Plenum Press, New York.

Allison, P.A. and Briggs, D.E.G. (1993) Exceptional fossil record: distribution of soft-tissue preservation through the Phanerozoic. *Geology* **21**, 527–530.

Briggs, D.E.G. (1995) Experimental taphonomy. *Palaios* **10**, 539–550.

Briggs, D.E.G. (1999) Molecular taphonomy of animal and plant cuticles: selective preservation and diagenesis. *Philosophical Transactions of the Royal Society of London B* **354**, 7–17.

Orr, P.J., Briggs, D.E.G. and Kearns, S.L. (1998) Cambrian Burgess Shale animals replicated in clay minerals. *Science* **281**, 1173–1175.

Seilacher, A. (1999) Biomat-related lifestyles in the Precambrian. *Palaios* **14**, 86–93.

Seilacher, A., Reif, W.-E. and Westphal, F. (1985) Sedimentological, ecological and temporal patterns of fossil Lagerstätten. *Philosophical Transactions of the Royal Society of London B* **311**, 5–23.

Wilby, P.R. and Briggs, D.E.G. (1997) Taxonomic trends in the resolution of detail preserved in fossil phosphatized soft tissues. *Geobios, Mémoire Spécial* **20**, 493–502.

3.4.2 Precambrian Lagerstätten

A.H. KNOLL and SHUHAI XIAO

Introduction

The perception that protists and prokaryotes, tiny and fragile, are unlikely candidates for fossilization gives rise to the view that the entire Precambrian fossil record is a string of minor miracles, unexpected triumphs of preservation over decay, oxidation, and metamorphism. The truth, however, is more prosaic. Algal cysts and bacteria are widely distributed in Phanerozoic rocks, making their occurrence in older cherts and shales more of an expectation than an enigma. Most Precambrian fossil assemblages contain simple remains that only hint at a wider diversity left unrecorded; true Lagerstätten are as rare in Archaean and Proterozoic successions as they are in younger rocks. For this reason, those few assemblages that bring ancient diversity into relatively sharp focus deserve the disproportionate attention that they have received.

An Archaean Lagerstätte

The fossil record recovered to date from rocks older than 2100 Ma is poor—far too meagre to support more than broad generalizations about early life (see Section 1.1.3). With this in mind, microfossils preserved in silicified grainstones of the 3450–3470 Ma Apex cherts, Warrawoona Group, Western Australia, qualify as the Earth's oldest Lagerstätte (Schopf 1993). Within the Warrawoona package, sedimentary rocks are subordinate constituents of a predominantly volcanogenic succession; sediments accumulated locally in a restricted coastal embayment and were pervasively altered by hydrothermal silicification soon after deposition. Compared with Proterozoic assemblages, the Apex fossils are not very impressive—a few more than 100 specimens of simple filaments that plainly show the effects of diagenesis. Yet, in the sea of darkness that surrounds them, the Apex fossils are a beacon, a sure sign that life existed nearly 3500 Ma. Schopf (1993) pointed out similarities between the preserved fossils and filamentous cyanobacteria. This interpretation may be correct, an indication that life had already gained molecular complexity and considerable phylogenetic diversity by the time the Apex cherts formed. On the other hand, the fossils are not diagnostically cyanobacterial and Warrawoona carbon isotopes, while consistent with the presence of oxygenic photosynthesis, do not require this interpretation. Compounding the difficulties of interpretation, Warrawoona and

other Archaean stromatolites, long regarded as the accreted products of cyanobacterial communities, provide uncertain evidence of microbial mats, cyanobacterial or otherwise. From the Warrawoona record, then, we can infer that 3500 Ma, life already characterized our planetary surface. Autotrophs, and probably photoautotrophs, fuelled ecosystems, and these primary producers may have included cyanobacteria. Regardless of whether or not cyanobacteria existed in the Warrawoona ocean, however, it is likely that contemporary ecosystems were characterized by physiologically complex and metabolically diverse bacteria and archaeans. Carbon isotopic evidence from ≈3900 Ma rocks in Greenland is consistent with an even earlier origin of autotrophy.

Proterozoic Lagerstätten

In contrast to that of the Archaean, the palaeontological record of Palaeoproterozoic and Mesoproterozoic life is abundant and well preserved (Knoll 1996). Preservation is especially good in silicified tidal flat carbonates characterized by syndepositional lithification and, at least locally, sea-floor carbonate precipitation. Mat-building populations of entophysalid cyanobacteria are preserved along with short oscillatorian trichomes and (in some cases) elongate akinetes, the resting stages of nostocalean cyanobacteria (Fig. 3.4.2.1) (Sergeev *et al.* 1995). The latter are particularly noteworthy in that both morphological and molecular phylogenies indicate that the Nostocales were the last major group of cyanobacteria to emerge. Nostocalean cyanobacteria are characterized by heterocysts, specialized cells that allow nitrogen fixation to take place in oxygen-rich environments. Geochemical data suggest that pO_2 first exceeded about 1% of present-day atmospheric levels 2200–2100 Ma, creating selection pressure for heterocyst evolution. Thus, by the time we see a well-preserved fossil record, much of the modern diversity of cyanobacteria must already have existed.

Simple acritarchs and sterane biomarker molecules in late Palaeoproterozoic shales tell us that eukaryotic cells were part of contemporary ecosystems, although their apparent diversity is low (Fig. 3.4.2.2f). Compressions of macroscopic organisms—notably the helical *Grypania*—and casts and moulds of macroscopic articulated organisms that resemble chains of beads provide a tantalizing glimpse of some early expressions of eukaryotic multicellularity.

Despite the early appearance of eukaryotes, it is not until the late Mesoproterozoic and Neoproterozoic eras that fossil assemblages document protistan diversification and the evolution of crown groups within the main algal clades. Silicified carbonates in a ≈1200 Ma platform succession from Arctic Canada contain abundant, cellularly preserved filaments of bangiophyte red algae (Fig. 3.4.2.2g). Bangiophyte populations attached themselves to a rippled hardground surface within the tidal zone and were subsequently inundated by carbonate mud; early diagenetic silica emplacement ensured the long-term preservation of the fossils.

Exceptionally preserved eukaryotic fossils in the ≈1000 Ma Lakhanda Formation, south-eastern Siberia, accumulated under different circumstances: burial beneath a veneer of clay-rich mud in a quiet subtidal marine setting. The relatively diverse Lakhanda assemblage includes both protists and prokaryotes, but is especially notable for the preservation of xanthophyte algae closely related to modern *Vaucheria* (Fig. 3.4.2.2a; the xanthophytes are a sister group to the brown algae).

Green algae are first found in Neoproterozoic rocks, but populations from another subtidal mudstone Lagerstätte in the 800–725 Ma Svanbergfjellet Formation, Spitsbergen, already include late-branching members of this clade (Fig. 3.4.2.2c) (Butterfield *et al.* 1994). Some acritarchs as old as 1000 Ma are also reasonably, if not unambiguously, interpreted as the vegetative spore walls of prasinophyte green algae (Fig. 3.4.2.2b). More generally, morphologically complex (acanthomorphic) acritarchs first appear in ≈1300–1200 Ma shales (Fig. 3.4.2.2h), and diversify through the Neoproterozoic Era. Consistent with this fossil record, diverse eukaryotic biomarkers characterize Neoproterozoic bitumens. When integrated with molecular phylogenies for the Eukarya, these records indicate: (1) that a rapid divergence of major eukaryotic clades took place 1300–1000 million years ago; (2) that both the primary endosymbiosis of cyanobacteria and protists that gave rise to photosynthesis in red and green algae and the secondary endosymbiosis between a unicellular alga (closely related to the modern reds) and a protistan host that gave rise to the photosynthetic stramenopiles (brown algae, diatoms, xanthophytes, and chrysophytes) took place more than 1000 million years ago; and (3) that multicellularity evolved early within the red, green, and stramenopile algae.

Perhaps the greatest of all Proterozoic Lagerstätten can be found in the 570 ± 20 Ma Doushantuo Formation, China (Fig. 3.4.2.3). This formation, which dates from the base of the Ediacaran interval, is widely distributed on the South China Platform. Nodular cherts in Doushantuo carbonates preserve diverse acritarchs and prokaryotes, but the true diversity of Doushantuo life is revealed in two distinct Lagerstätten, one in carbonaceous shales that cap the formation in the Yangtze Gorges area (Steiner 1994) and a second in phosphorites exposed near Weng'an in Guizhou Province. Compressions in uppermost Doushantuo shales include at least two dozen taxa of multicellular algae and, perhaps, Ediacaran-grade

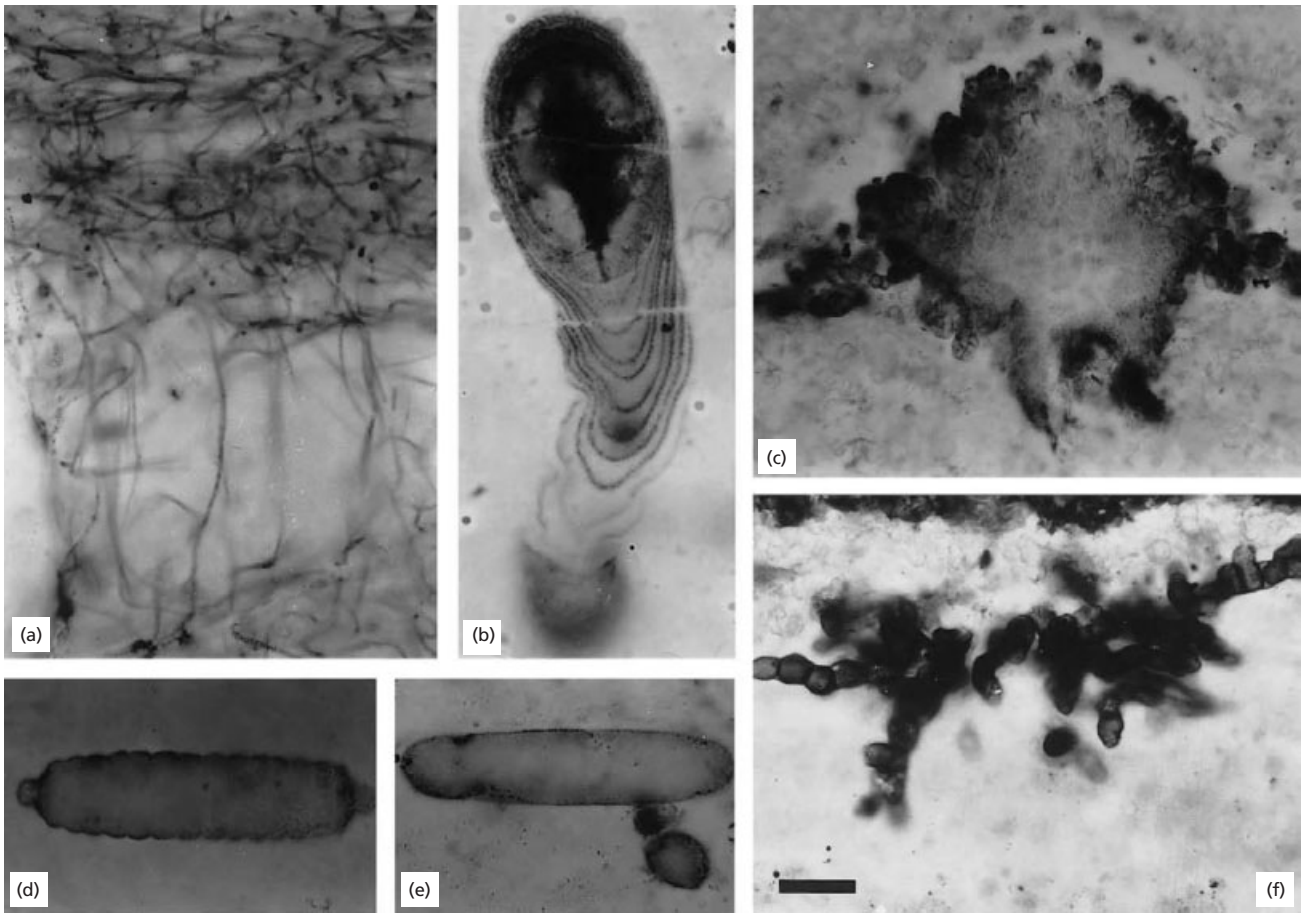
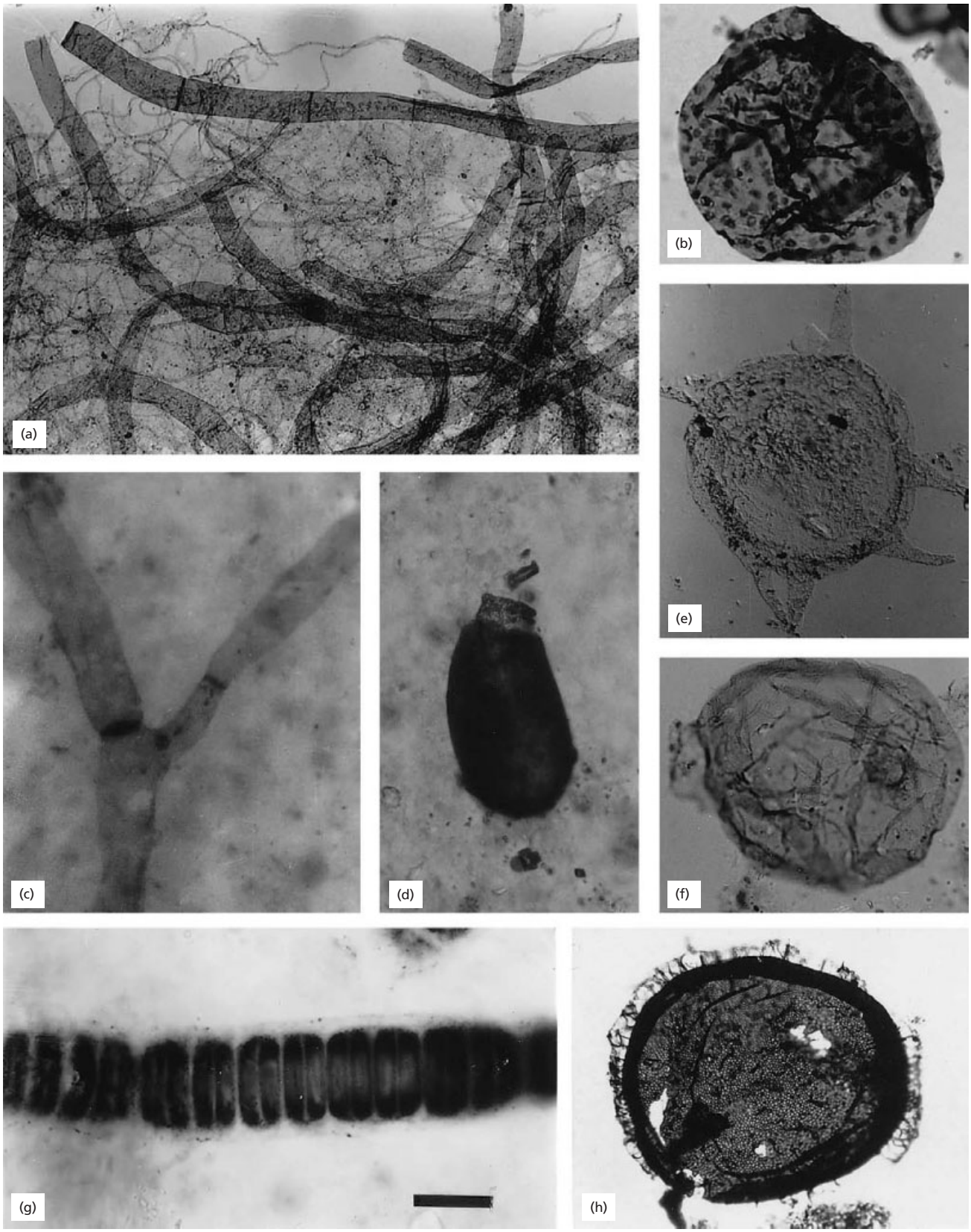


Fig. 3.4.2.1 Prokaryotic microfossils in silicified Proterozoic carbonates. (a) Mat-building cyanobacteria showing characteristic alternation of vertically and horizontally orientated filaments, Neoproterozoic Backlundtoppen Formation, Spitsbergen. (b) *Polybessurus*, a stalk-forming cyanobacterium common in Mesoproterozoic and Neoproterozoic tidal flats characterized by carbonate muds, Neoproterozoic Draken Formation, Spitsbergen. (c) *Eoentophysalis*, a mat-building coccoidal cyanobacterium common in Palaeoproterozoic and Mesoproterozoic tidal flats characterized by firm substrates and rapid carbonate lithification, Mesoproterozoic Billyakh Group, Siberia. (d) *Filiconstrictosus*, a short, presumably oscillatorian cyanobacterium, Billyakh Group. (e) *Archaeoellipsoides*, the preserved akinete of a nostocalean cyanobacterium, Billyakh Group. (f) *Eohyella*, an endolithic cyanobacterium preserved in silicified ooids of the Neoproterozoic Upper Eleonore Bay Group, Greenland. Bar in (f): 50 µm for (a) and (f); 15 µm for (b); 30 µm for (c); and 20 µm for (d) and (e).

animals. Notable among the compression populations is *Miaohephyton*, a dichotomously branching thallus whose preserved details of growth and reproductive biology suggest that it may be a brown alga (Fig. 3.4.2.3d).

Doushantuo phosphorites accumulated across a broad, latest Proterozoic marine platform, but are best developed adjacent to inferred emergent land masses. As in younger phosphorite deposits, sediment starvation, high productivity, oxygen-poor bottom waters, and bacterial mats all appear to have played a role in deposition; and, like younger phosphatic fossils, Doushantuo specimens are encrusted by an isopachous rim of finely crystalline apatite, with cell interiors commonly filled by

Fig. 3.4.2.2 (*Facing page*) Eukaryotic microfossils preserved in Proterozoic cherts and shales. (a) Xanthophyte alga in shales of the ≈ 1000 Ma Lakhanda Formation, Siberia. (b,e,f,h) Acritarchs from: (b) early Neoproterozoic Miroyedikha Formation, Siberia; (e) late Neoproterozoic Kursovsky Formation, Siberia; (f) Mesoproterozoic Roper Group, Australia; and (h) Mesoproterozoic Beidajian Formation, China. (c) Green alga from the Neoproterozoic Svanbergfjellet Formation. (d) Vase-shaped protist from the Neoproterozoic Elbobreen Formation, Spitsbergen. (g) Bangiophyte red alga from the Mesoproterozoic Hunting Formation, Arctic Canada. Bar in (g): 100 µm for (a); 15 µm for (b) and (f); 25 µm for (c), (d), and (g); 50 µm for (e); and 75 µm for (h).


(a)
(b)
(c)
(d)
(e)
(f)
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(h)

collophane. None the less, the mechanistic basis of phosphate permineralization remains poorly understood. Doushantuo phosphorites contain abundant acritarchs (Fig. 3.4.2.3a,f) as well as cellularly preserved algal thalli whose multiaxial development, differentiation of cortical and medullary tissues, and reproductive bodies indicate affinities with florideophyte red algae (Fig. 3.4.2.3b,e). Perhaps most remarkable, phosphatized fossils also include animal embryos preserved in the early stages of cleavage (Fig. 3.4.2.3c) (Xiao *et al.* 1998).

Doushantuo fossils confirm that by the time Ediacaran animals enter the fossil record, multicellular red, green, and stramenopile algae had already diversified to produce much of the architectural and reproductive variation seen within these groups today. Doushantuo embryos provide our first, tantalizing glimpse of microscopic, soft-bodied animals, holding out the promise of a pre-Ediacaran record of microscopic animals that may capture some of the earliest events in metazoan evolution.

Conclusions

The Precambrian palaeontological record continues to expand, revealing new and sometimes unanticipated aspects of the Earth's early biological diversification. Lagerstätten that preserve ancient organisms in vegetative and reproductive detail are particularly valuable in the effort to integrate evolutionary perspectives drawn from geology and comparative biology. Frontiers in Precambrian research include: (1) the fuller documentation of algal and early animal diversity in Neoproterozoic

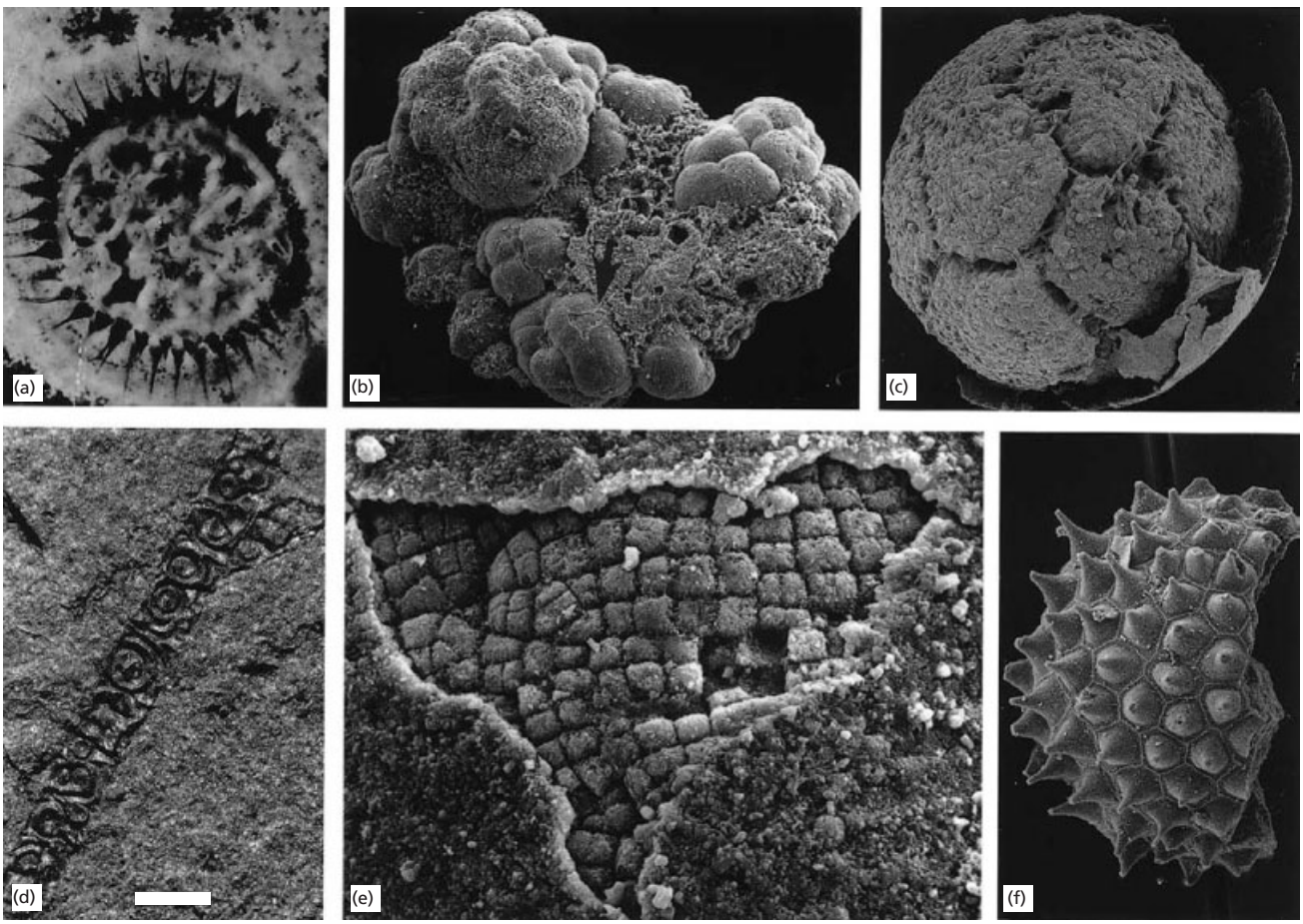


Fig. 3.4.2.3 Compressed and phosphatized fossils from Lagerstätten in the Neoproterozoic Doushantuo Formation, China. (a,f) Optical and SEM micrographs of acanthomorphic acritarchs. (b,e) SEM micrographs of a red algal thallus; (e) is a high magnification view showing cell surface pattern on the thallus illustrated in (b) (position noted by arrow). (c) Blastomeres in a phosphatized animal embryo. (d) *Miaohephyton*, a carbonaceous compression tentatively assigned to the brown algae; note circular conceptacles on thallus surface. Bar in (d): 50 µm for (a) and (f); 160 µm for (b); 100 µm for (c); 450 µm for (d); and 10 µm for (e).

rocks, including the records of both radiation and extinction; (2) the documentation of early eukaryotic evolution in Palaeoproterozoic and Mesoproterozoic successions; and (3) the search for fossils, biologically mediated petrological textures, and biomarker molecules in Archaean rocks, especially in preserved hydrothermal precipitates.

Perhaps our most stimulating future opportunities lie in the participation of palaeontologists and biogeochemists in renewed solar system exploration, with careful collection and investigation of ancient Martian sediments forming the logical extension of efforts to understand the palaeontological record of early life on Earth.

References

Butterfield, N.J., Knoll, A.H. and Swett, K. (1994) Paleobiology of the Upper Proterozoic Svanbergfjellet Formation, Spitsbergen. *Fossils and Strata* **34**, 1–84.

Knoll, A.H. (1996) Archean and Proterozoic paleontology. In: J. Jansonius and D.C. McGregor, eds. *Palynology: principles and applications*, Vol. I, pp. 51–80. American Association of Stratigraphic Palynologists Foundation, Tulsa.

Schopf, J.W. (1993) Microfossils of the early Archean Apex chert: new evidence of the antiquity of life. *Science* **260**, 640–646.

Sergeev, V.N., Knoll, A.H. and Grotzinger, J.P. (1995) Paleobiology of the Mesoproterozoic Billyakh Group, northern Siberia. *Paleontological Society Memoir* **39**, 1–37.

Steiner, M. (1994) Die Neoproterozoischen Megaalgen Südchinas. *Berlin Geowissenschaftliche Abhandlungen (E)* **15**, 1–146.

Xiao, S., Zhang, Y. and Knoll, A.H. (1998) Three-dimensional preservation of algae and animal embryos in a Neoproterozoic phosphorite. *Nature* **391**, 553–558.

3.4.3 Chengjiang

J. BERGSTRÖM

Introduction

The Chengjiang Lagerstätte, discovered by Hou Xianguang in 1984, is one of the oldest Lagerstätten with soft-bodied preservation. It falls in the *Micrhystridium dissimilare* acritarch Zone, corresponding to the Middle-to-Upper Tommotian in Siberia, to the Vergale in the East Baltic, and to the *Holmia kjerulfi* Zone in Baltoscandia (Hou and Bergström 1997). This equates with about the middle of the Lower Cambrian, or perhaps slightly lower, its top being dated ≈525 Ma. Because of this Early Cambrian age, the Chengjiang Lagerstätte has the potential to elucidate the earliest Phanerozoic diversification of animals.

Sedimentary environment and diagenesis

Evidence from a drill core shows that the lithology is mainly a grey mudstone without obvious bedding. It weathers at the surface to a light grey to yellow colour. There are some centimetre-thick sheets of sand or silt covered by laminated muds, indicating deposition in a prodelta setting, but these sandy units appear to extend only a few tens of metres. Ripples and sole marks have been observed, and there are also occasional storm beds with hummocky crossbedding. It has been suggested that turbiditic mud-flows carried the organisms into a low-oxygen environment. This interpretation is consistent with their excellent preservation. However, the fossils do not usually occur where the bedding shows the influence of storms or slumping, but in parts of the sequence where the sediment is a notably homogeneous, even-grained, grey mudstone. This uniform sediment dominates the sequence that yields the Chengjiang fauna. The high degree of sorting indicates that the mud was probably derived from wind-transported sediment, and the depositional environment may have been a continental slope basin offshore from an estuary, into which large amounts of sediment were washed after heavy rains and flooding (Lindström 1995).

The homogeneity of the sediment may have made trace fossils difficult to observe but, since the body fossils are largely undisturbed, it is more likely that there was very little burrowing activity. The fossils are neither inclined to the horizontal nor distorted, as they are in the turbidites of the Burgess Shale and the Hunsrück Slate (see Section 3.4.6); nor are they clustered and entangled together, or generally concentrated along distinct horizons. Instead, they are flat-lying. Linguloid brachiopods occur with the pedicle extending into the underlying sediment, indicating that they are probably preserved in life position. The composition of the fauna, and the normal development of eyes in the arthropods, is consistent with deposition in a relatively shallow marine environment. Bentonitic clay has been reported from the fossiliferous levels, suggesting that the soft-bodied fauna may have been killed and embedded in possibly toxic, volcanic ash.

Biota

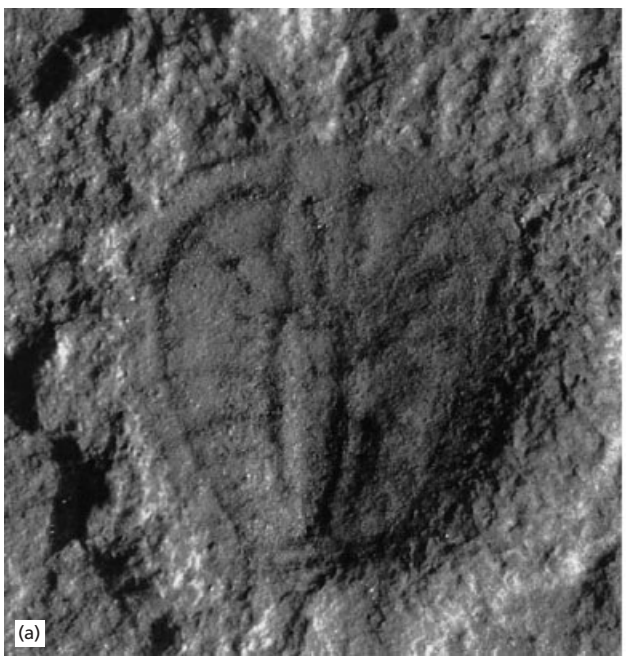
The fossils occur on smooth cleaved surfaces, or they can be exposed by careful preparation. In many specimens only an impression survives. Often the colour of the fossils matches that of the surrounding rock; in other cases there is a clear contrast, e.g. the worm *Yunnanozoon* is always grey. Details may be revealed in polarized light

(Fig. 3.4.3.1). Thicker coloured material characterizes some of the arthropods, its composition usually modified by weathering. There is evidence of both phosphatization and some pyritization of shells and skeletons.

Arthropods dominate the fauna (Table 3.4.3.1), making up about 45% of the species diversity; sponges account for 20% and other taxa only 35%. There are strong similarities with the Burgess Shale fauna, in which arthropods make up about 43% of the fauna, sponges about 20%, and the rest just 37%. The similarities are not restricted to these proportions; many species from the two faunas are closely related, and are assigned to the same genera or families. However, there are also differences: notably the Chengjiang fauna includes six common species of ostracode-like bradoriid arthropods, whereas there is only one rare species in the Burgess Shale. The Burgess Shale fauna includes five echinoderms and some molluscs; neither phylum is yet known with certainty from Chengjiang. Aschelminth worms are present in both faunas, but whereas those in the Burgess Shale are described as priapulids, most of the examples in the Chengjiang fauna are more similar to nematomorphs. The Chengjiang worms have stiff, slender bodies, bending in very regular S-curves like extant nematodes and nematomorphs, whereas the Burgess Shale forms are commonly bag-like and irregularly bent (and a few secrete a tube). This indicates a fundamental difference in the musculature of the body wall. Since the two groups are probably closely related, there may be species that are more or less intermediate.

Similarities are also found with other faunas, such as that from the Middle Cambrian of Utah. This has a much larger proportion of trilobites and agnostids (72 species, making up 43% of the metazoans) than the Burgess Shale (19 species, 12%) and Chengjiang (3 species, 3%) faunas. The Chengjiang fauna includes 12 lamellipedians (trilobitomorphs) other than trilobites, the Burgess Shale fauna seven, and the Utah fauna one; of these, naraoiids are characteristic components of the first two faunas, but appear to be rare in Utah. The significance of this difference is uncertain. Communities may not have been as distinct as they are today, with many species distributed across several. The contrast in species composition indicates that the Chengjiang, Burgess, and Utah faunas were discrete communities, but the similarities indicate that at least the Chengjiang and Burgess Shale communities represent related (naraoiid) communities.

It is safe to assume that modes of feeding during the Cambrian (see Section 1.2.3) were the same as those in the living members of several groups, such as sponges and brachiopods; the phyla were already remarkably advanced at this early stage. Among many arthropods, however, the lack of true mouthparts suggests a mud-eating habit; the gut of at least 12 of the ≈30 non-bradoriid and non-trilobite genera is commonly mud-



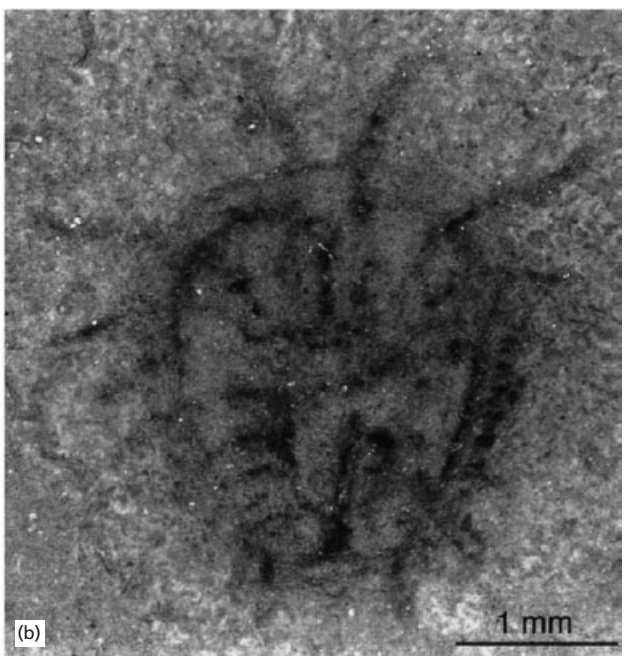


Fig. 3.4.3.1 Larva of the trilobite-like arthropod *Naraoia spinosa* Zhang and Hou 1985. Photographed without (a) and with (b) a polarizing filter; note antennae and other appendages preserved as a thin organic film. (From Hou and Bergström 1997.)

Table 3.4.3.1 Composition of the Chengjiang fauna.

Animal group	Number of species
Sponges	≈20
Possible cnidarians	2
Ctenophores	1
Nematomorphs and priapulids	4
Anomalocaridids	4
Brachiopods	4
Annelids	1
Lobopodians	6
Arthropods:	42
Trilobites	3
Trilobite-like forms	13
Bradoriids	6
Others	20
Hyoliths	3
Molluscs	—
Echinoderms	—
Total	≈87

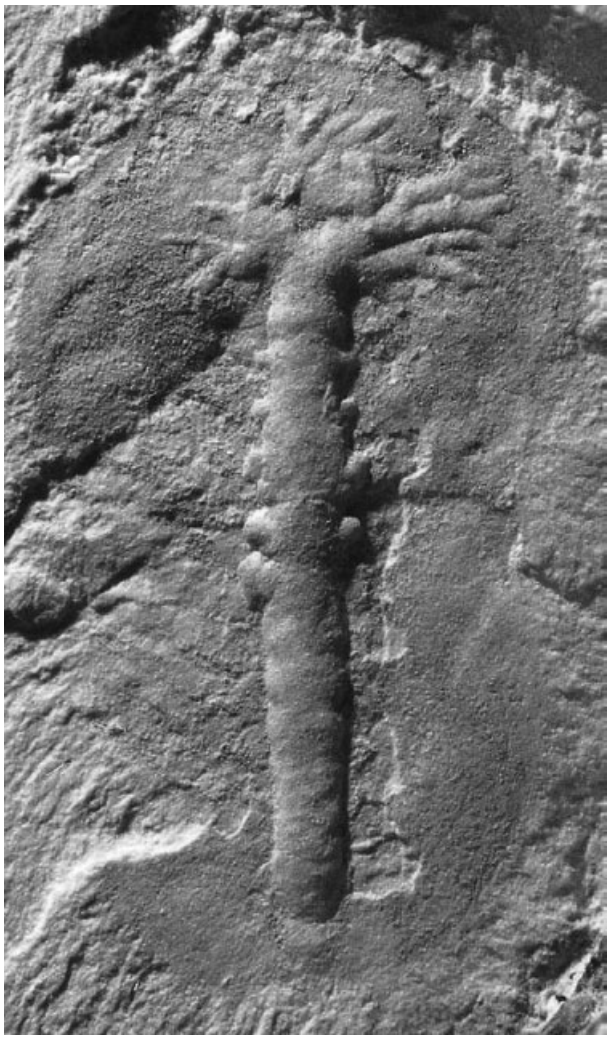


Fig. 3.4.3.2 *Naraoia spinosa* Zhang and Hou 1985, with wide mud-filled gut and diverticula, ×16.

filled (Hou and Bergström 1997) (Fig. 3.4.3.2). Mud-eating is rare among extant arthropods. Arthropods such as the megacheirans ('big-hands') and anomalocaridids developed notable grasping appendages (≈10 species). These lack traces of mud in the gut, so the appendages represent an early adaptation to a scavenging or carnivorous feeding habit. There is no reliable evidence of more sophisticated adaptations for filtering small particles, but if the identification of some species as branchiopod crustaceans is correct, such devices probably existed. The mud-eating habit occurred in a number of discrete arthropod groups. As a rule it is associated with a lack of tagmosis in the appendages—only the antennae are differentiated. This indicates that mud-eating was inherited from prearthropod ancestors, and abandoned in association with the differentiation of specialized head appendages.

Interpretations of mode of feeding may be influenced by the likely systematic position of the animal in question. For instance, the two eldonioid species *Eldonia eumorpha* and *Rotadiscus grandis* have been regarded as medusae and therefore as carnivores. They were formerly interpreted as planktic animals that were overwhelmed in great numbers by turbidity currents and deposited in 'colonies' (Chen *et al*. 1995). The realization that they had a spiral gut and bilaterally arranged tentacles led to their reinterpretation as ciliary feeders. The heavy shell of *Rotadiscus* suggests that it lay with its shell on the bottom (Dzik *et al*. 1997). This interpretation is supported by the ciliary mode of feeding, the lack of evidence for turbidity currents, and the small likelihood that a pelagic animal could have been swept up in large numbers by a bottom current. Lobopods are commonly found associated with eldonioids; they may have had some kind of symbiotic relationship, or they may have fed on dead or live individuals.

References

Chen, J.-y., Zhu, M.-y. and Zhou, G.-q. (1995) Anatomy and phylogenetic relationships of the medusiform Eldonioidea. In: J.-y. Chen, G. Edgecombe and L. Ramsköld, eds. *International Cambrian Explosion Symposium* (April 1995, Nanjing), Programme and abstracts, pp. 9–10.

Dzik, J., Zhao, Y.-l. and Zhu, M.-y. (1997) Mode of life of the Middle Cambrian eldonioid lophophorate *Rotadiscus*. *Palaeontology* **40**, 385–396.

Hou, X.-g. and Bergström, J. (1997) Arthropods of the Lower Cambrian Chengjiang fauna, southwest China. *Fossils and Strata* **45**, 1–116.

Lindström, M. (1995) The environment of the Early Cambrian Chengjiang fauna. In: J.-y. Chen, J.G. Edgecombe and L. Ramsköld, eds. *International Cambrian Explosion Symposium* (April 1995, Nanjing), Programme and abstracts, p. 17.

3.4.4 The Soom Shale

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Introduction

The Soom Shale Member is a 10–15 m thick argillaceous unit within 3000 m of arenites that make up the Cambrian–Silurian Table Mountain Group of the southwestern Cape Province, South Africa. It is of latest Ordovician (Ashgill) age, and comprises thinly laminated siltstones and mudstones that are black when fresh, but weather to a pale grey colour. The shale crops out as a recessive level throughout the Cedarberg Mountains, but is highly deformed in the region east of Cape Town. To the north of Cape Town, especially in the area around Clanwilliam, several localities expose relatively undeformed Soom Shale, and it is these that have yielded exceptionally preserved fossils (Aldridge *et al.* 1994). The special feature of the shale is the preservation of fossilized soft tissues as clay mineral replacements (Gabbott 1998). The biota includes conodonts, brachiopods, orthocone cephalopods, arthropods, algae, and a number of enigmatic animals.

Sedimentary environment

During the Late Ordovician, the southern tip of Africa was at a latitude of about 60°S, and the Soom Shale was deposited under the influence of the glacial episode that widely affected the southern Gondwanan continents at that time. The shale is directly underlain by tillites of the Pakhuis Formation, and there are occasional dropstones, particularly near the base of the shale, providing evidence of at least some ice cover. The depositional environment has been interpreted as being within a quiet water basin close to the retreating ice front. The mud and silt laminae are normally less than 1 mm thick, rarely up to 10 mm; they are laterally persistent and undisturbed by any current activity or bioturbation. They appear to have been deposited by the settling of fine, perhaps wind-blown, detritus from suspension. Many of the bedding planes are covered with algal ribbons, and there is a possibility that the sediment surface was bound by microbial mats. Above the Soom Shale, the siltstones and fine sandstones of the Disa Siltstone Member display sedimentary structures that testify to an increasing importance of wave and current activity within the basin.

Several lines of evidence—most notably the parallel-laminated, non-bioturbated sediment, the preponderance of nektonic and necktobenthic organisms, and the sedimentary geochemistry—indicate that the bottom waters in which the Soom Shale accumulated were dominantly anoxic or euxinic with brief periods of oxygenation.

Biota

The fauna of the Soom Shale is characterized by nektonic and necktobenthic species; conodonts are particularly common (Aldridge *et al.* 1994). The conodonts are represented by isolated elements and, more commonly, by partial or complete feeding apparatuses; several of the apparatuses have associated soft tissues, especially traces interpreted as representing the eyes (Fig. 3.4.4.1a), and a single more complete conodont animal, preserving eye and trunk musculature, has been discovered (Gabbott *et al.* 1995). The conodont elements are all extremely large, commonly 10–20 mm in length, and are referable to a single species, the prioniodontid *Promissum pulchrum*. Other nektonic fossils include a *Jamoytius*-like naked agnathan and orthoconic cephalopods, the latter being commonly encrusted by lingulate brachiopods and cornulitids. Isolated lingulate brachiopods, including rare specimens of *Lingula*, and occasional ribbed articulate brachiopods also occur. Arthropods are represented by the eurypterid *Onychopterella*, the naraoiid *Soomaspis*, the trilobite *Mucronaspis*, myodocopid ostracods, and possible phyllocarids; all of these were probably nektobenthic. Soft tissues are particularly well preserved in several of the eurypterid specimens, which display musculature and book-gills. The fauna also contains a number of enigmatic forms, some of which are soft-bodied and difficult to assign to a phylum (Fig. 3.4.4.2); additionally, there are numerous scattered organic-walled spines (*Siphonacis*) of unknown affinity. Chitinozoans are abundant on some bedding planes as scattered individuals, large clusters, long chains, or associated with cocoons. Palynological preparations of the shale have produced additional chitinozoans, as well as simple spores and spherical acritarchs.

In addition to providing a rare Ordovician Konservat-Lagerstätte, the Soom Shale preserves a unique early Palaeozoic cold-water community. There is an apparent

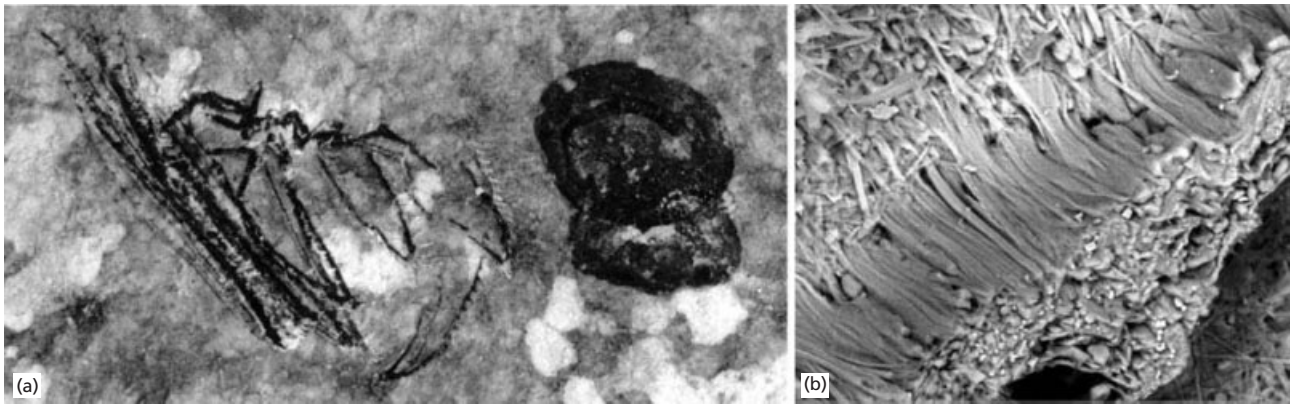

Fig. 3.4.4.1 Preservation of conodont features in the Soom Shale. (a) Complete feeding apparatus, mostly mouldic, with eye capsules preserved as carbonized films; anterior to right, ×9. (b) Scanning electron micrograph of muscle fibres associated with eye capsules on another specimen, preserved as clay mineral replications, ×560.

dominance of vagile predators and scavengers (conodonts, orthocones, large arthropods), with only the brachiopods and cornulitids evidently occupying a filter-feeding niche. The common habit of the lingulate brachiopods as pseudoplanktic epibionts on orthocone shells attests to an inhospitable or barren sea-bottom environment. The myodocopid ostracods are mostly found in association with the orthocone conches, on which they may have been scavenging. There is evidence for the presence of undiscovered large predators or scavengers in the fairly common occurrence of coprolites containing crushed orbiculoid shells or fragmentary conodont elements.

Taphonomy

The Soom fossils show a remarkable level of preservation, sometimes with three-dimensional features of the soft tissues intact. As the majority of the fauna was nektonic or nektobenthic, some carcasses must have sunk rapidly to the sea floor after death; there is no evidence to suggest that any significant transport took place before deposition. Scavengers would have been excluded from the sediment surface during those periods when the bottom-water conditions were dominantly anoxic or euxinic. However, decomposition of the soft tissues by anaerobic bacteria would have destroyed the carcasses completely unless rapid mineralization occurred. The soft tissues and some of the hard tissues are now preserved in clay minerals, and the high quality of replication (Fig. 3.4.4.1b), sometimes even conserving subcellular features, strongly suggests that clay minerals were directly involved in the replacement of animal tissues. There is no evidence for the occurrence of any preliminary phase of mineralization involving phosphate, pyrite, or calcite. The highly acidic geochemical environment at the time of deposition would have aided clay mineral/organic interactions whilst militating against phosphate, pyrite, or carbonate interactions with the organic material (Gabbott 1998).

Colloidal clay particles have an affinity for organic substrates in the presence of cations (see Theng 1979 and references therein). This affinity, coupled with the small (1 µm to 1 nm) particle size of colloidal clays, offers the potential for high-fidelity soft-tissue replication. In the Soom Shale basin, detrital illite and kaolinite, and possibly authigenic kaolinite, probably existed as colloidal suspensions in the pore and bottom waters. These particles probably would have had net negative charges under the low pH conditions present, as would any organic substrate (i.e. the soft tissues of animals). Therefore, before any interaction between the clay minerals and the organic substrate could occur, their mutual electrostatic repulsion had to be overcome. Attractive forces, either chemical or physical, could then operate. For example, in the presence of electrolytes such as Na^+ and Ca^{2+} clay minerals would have been able to approach the organic substrate closely enough to bond by van der Waals and/or hydrogen bonding (Theng 1979). In this way, colloidal clay minerals could have nucleated by flocculation and subsequently become adsorbed on to specific organic substrate templates so that the soft tissues were replicated before they were destroyed.

The labile, decay-susceptible tissues such as muscle show the most detailed preservation, whereas more recalcitrant organic tissues such as the chitin of eurypterid carapaces are replaced without the same level of detail. In addition to the clay replication, there is some organic preservation in the form of carbon films, which are evident, for example, in the conodont eyes and the *Siphonacis* spines; this form of preservation is rarer than the clay replication. In some cases, most notably the

Fig. 3.4.4.2 A large, enigmatic, segmented, soft-bodied animal, preserved in the Soom Shale by clay mineral replacement, ×0.3.

conodont eye capsules, both organic and clay mineral preservation co-occur where the clays have coated the surface of the organic substrate. It is the most recalcitrant organic biomolecules that show organic preservation, indicating perhaps that the reactivity of the organic substrate controlled the process of clay mineralization, with the labile tissues preferentially acting as templates for the clay particles that eventually replaced them. During diagenesis, the compositions of the clays have been modified and now lie in the illite and mixed layer clay solid solution series.

While the acidic bottom waters appear to have promoted the replacement of soft tissues by clay minerals, they served to dissolve completely the skeletal biominerals of the animals. The aragonite of the orthocone cephalopods, the calcite of the trilobites and articulate brachiopods, and even the apatite of conodont elements and lingulate brachiopod shells have all disappeared. The demineralization of the apatite, in particular, is indicative of very low pH waters.

The unusual early diagenetic history of the hard and soft parts of the organisms was largely controlled by the composition of the organic and sediment matter supplied to the sea floor, which in turn controlled the Eh–pH conditions of the ambient waters. The presence of large quantities of organic matter is evident from the masses of algal material on many bedding planes. Decomposition of this organic matter by sulphate-reducing bacteria in an environment with limited reactive iron oxides would have produced pore and bottom waters rich in H_2S. This acidity may have been exacerbated by oxidation of the H_2S to form sulphuric acid. The sparsity of carbonate-bearing minerals meant that there was no available pH buffer, allowing large-scale dissolution of the biominerals, inhibiting phosphatization and pyritization of the soft tissues, but encouraging clay mineral replacement of organic tissues.

References

Aldridge, R.J., Theron, J.N. and Gabbott, S.E. (1994) The Soom Shale: a unique Ordovician fossil horizon in South Africa. *Geology Today* **10**, 218–221.

Gabbott, S.E. (1998) Taphonomy of the Upper Ordovician Soom Shale lagerstätte: a unique example of soft tissue preservation in clay minerals. *Palaeontology* **41**, 631–637.

Gabbott, S.E., Aldridge, R.J. and Theron, J.N. (1995) A giant conodont with preserved muscle tissue from the Upper Ordovician of South Africa. *Nature* **374**, 800–803.

Theng, B.K.G. (1979) *Developments in soil science: formation and properties of clay–polymer complexes*. Elsevier, Amsterdam and New York.

3.4.5 The Rhynie Chert

N.H. TREWIN

Introduction

In the Rhynie chert a unique Early Devonian terrestrial ecosystem of plants and arthropods has been preserved in superb detail by the deposits of a hot-spring system. Rhynie is situated 50 km east-north-east of Aberdeen, in north-east Scotland, and fossiliferous cherts are restricted to a few small areas to the west of the village. There is no outcrop and all palaeontological research has been conducted on blocks found loose in the fields, or obtained by trenching or drilling. The cherts occur within the narrow north–south Rhynie Basin of Lower Old Red Sandstone which is faulted at the western

margin; strata rest unconformably on basement at the eastern basin margin. The cherts occur within a sequence of shales and sandstones near the base of the local succession. An andesitic lava flow, airfall tuffs, and tuffaceous sandstones occur in close association with the chert-bearing strata.

The age of the chert is Pragian (Early Devonian) on the basis of palynology; a confirmatory radiometric age (Ar/Ar method) of 396 ± 12 Ma has been obtained for the chert (Rice *et al.* 1995).

The Rhynie environment

From the time of its discovery in 1912 and the classic work on the plants by Kidston and Lang (1917–21), authors have suggested that the Rhynie biota was preserved by the siliceous sinters of a hot spring. Recent research (Rice *et al.* 1995) has confirmed that the cherts form the surface expression of a precious-metal bearing hot-spring system. Characteristic chemical alteration of both country rock and Devonian deposits extends for over 1.7 km along the basin margin in the Rhynie area, indicating the activity of a system of substantial size during the waning period of local andesitic volcanism. A lava flow in the area is extensively altered to sericite and K-feldspar; tuffaceous material occurs scattered in discrete beds in shales and sandstones, and also as silicified and altered material in thicknesses of over 50 m which may have formed part of a tuff cone. A few altered volcanic clasts occur within the chert sequence.

The sedimentary succession containing the cherts (Dryden Flags and Shales and underlying sandstones) is of local extent. Drilling (in 1997) proved a succession of ≈200 m with dark green to grey shales, displaying desiccation cracks, rip-up clasts, ripple lamination, and thin graded laminae. Associated fine- to medium-grained sandstones are parallel and ripple laminated, and some beds are burrowed. The plant-bearing cherts generally rest on fine sandstones and were deposited subaerially as hot spring sinters from local vents. At Windyfield, 700 m from the main site, a fragmented chert with botryoidal texture typical of the splash zone around a geyser vent has been found (Trewin 1994). The hot-spring activity frequently disrupted and altered the sediments, and it fractured and resealed previously deposited cherts. Fossiliferous chert occurs as beds through at least 25 m of strata at the Rhynie site, and also as isolated pods at Windyfield.

The environment was an alluvial plain with shallow ephemeral pools which bordered a river flowing north. Drainage was probably modified locally by both the volcanic and hot-spring activity. The biota colonized subaerial surfaces and small shallow pools (Fig. 3.4.5.1). Hot-spring fluids periodically invaded these areas, resulting in death and silicification of the biota.

Preservation

The quality of preservation of the Rhynie biota is very variable (Trewin 1996) and only a small proportion of the chert beds contain perfectly silicified three-dimensional plant material in which details of cell structure are evident (Fig. 3.4.5.2). Two main factors are: (1) the quality of the silicification; and (2) the state of decay of the material prior to silicification. Plant and arthropod material is found silicified in all stages of decay; thus transported, degraded plant litter of autochthonous or allochthonous origin, showing breakdown of tissue structure and infestation by fungi, can be perfectly silicified, but the details of plant structure are best

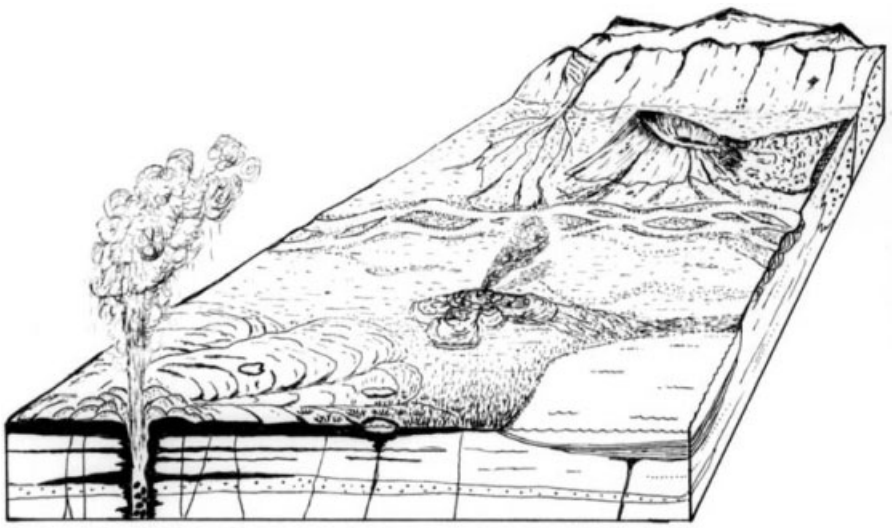

Fig. 3.4.5.1 Reconstruction of the Rhynie environment. Sinters from hot springs and geysers invade areas of plant growth adjacent to a lake on the alluvial plain of a braided river system. Clastic material of local origin is derived from adjacent uplands, and eroding volcanics also contribute debris.

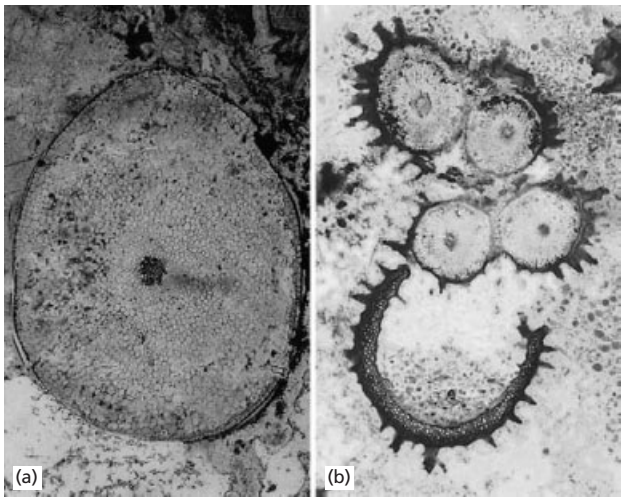

Fig. 3.4.5.2 (a) Silicified stem of *Rhynia* preserving cellular structure; Rhynie chert, ×10. (b) Plant axes, and crescentic fragment of decayed plant with geopetal fill; digitate microbial mat partly covers the plants which were silicified within a small pool; Windyfield chert, ×5.

revealed when growing plants were engulfed in the Si-rich hot spring waters. In some beds plant axes up to 15 cm long are preserved in the erect position of growth; in others germinating spores are present.

The hot spring fluids flooded areas where plants grew on a sandy substrate; chert beds grade rapidly down into compacted chert-cemented carbonaceous sandstone. Many chert beds are multiple, and plants colonized the sinter surface between hot-spring eruptions (Fig. 3.4.5.3). Silicification preserved the biota at specific moments; thus some beds contain young growing plants, some contain mature plants with spore cases and abundant spores in the chert matrix, and others contain mainly biologically degraded material and spores. Arthropods are found as complete individuals and fragments in the chert; occasionally trigonotarbids occur within empty spore cases or hollow stems. The small arthropods are frequently preserved in great anatomical detail, with sensory hairs still attached to pits in the cuticle.

Small pools on the sinter surface were colonized by freshwater crustaceans (*Lepidocaris*), aquatic algae (*Palaeonitella*), and bacterial mats which grew on plant fragments (Fig. 3.4.5.2b), some of which floated in the water. The invasion of such pools by hot spring water preserved the aquatic community.

The silicification process generally started with plant material being coated in amorphous silica. It proceeded from the outside of the stem by filling individual plant cells or replacing the contents with silica until the whole thickness of the stem was silicified. Organic cell wall material is still present in many beds, but in those subjected to hotter conditions it appears to have been burnt out and the resulting cavity may also be filled with silica. The silicification process frequently stopped when only the outer part of a stem was silicified, leaving a hollow centre where the organic material decayed. The various preservational features of plant stems can be compared with features commonly observed in modern hot-spring deposits (Trewin 1996).

Biota

The Rhynie biota comprises land plants, algae, fungi, a lichen, and bacterial mats, together with arthropods, which include a crustacean, trigonotarbid arachnids, a mite, and a collembolan (springtail). Other material includes centipede fragments and a euthycarcinoid.

Plants

The most abundant land plants are the spore-bearing sporophytes, which display an alternation of generations with sexual gametophytes. The small gametophytes of several plants have been described, in one case including the preservation of coiled sperm. The sporophytes were all less than 50 cm tall but formed laterally extensive sprawling clumps due to clonal growth. The plants had creeping horizontal axes, some of which bore hair-like rhizoids. Vertical stems with simple stomata rose from the horizontal axes. The stems were naked except in *Asteroxylon*, and bore either terminal or lateral sporangia which contained a single spore type. The Rhynie plants have simple organization and are the oldest land plants for which the detailed anatomy and complete life cycles are known; the taxonomic position of several genera is problematic (reviewed by Cleal and Thomas 1995).

Seven sporophyte genera are present: *Rhynia* and *Horneophyton* are assigned to the Rhyniaceae, *Asteroxylon* to the lycopsids, *Trichopherophyton* and an unnamed form to the Zosterophyllophytales, and *Aglaophyton* and *Nothia* are of uncertain affinities. Figure 3.4.5.3 shows typical forms of the common genera.

Algae are represented by the Chlorophyta and the aquatic charophyte *Palaeonitella*. The problematic Nematophytales are represented by *Nematophyton* and *Nematoplexus*. Fungi are represented by resting spores and hyphae of several kinds (see Section 4.2.9), and a parasitic relationship between an aquatic fungus and *Palaeonitella* has been described, as well as an example of mycoparasitism (parasitic relationship between fungi). The earliest known lichen also occurs in the chert (see Section 4.2.9).

Six cyanobacterial species have been described; small domal structures and mats associated with sinter surfaces and coating plant axes are also probably cyanobacterial in origin. Filaments 2–3 μm in diameter occur in

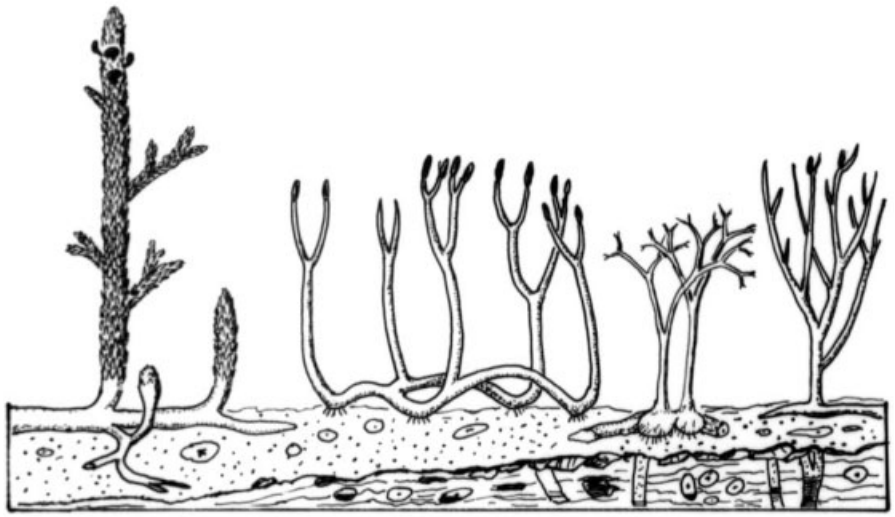

Fig. 3.4.5.3 Commoner plants of the Rhynie chert. From left to right: *Asteroxylon*, *Aglaophyton*, *Horneophyton*, and *Rhynia*. Height of *Aglaophyton* ≈ 200 mm. The plants are shown growing on a thin sandy substrate overlying a sinter with preserved plants of an earlier generation.

laminae about 0.2 mm thick which comprise filaments orientated alternately vertical and horizontal (typical of a phototactic control).

Arthropods

The small freshwater crustacean *Lepidocaris* is common locally in chert that resulted from the silicification of biota in small pools. The Chelicerata are represented by the trigonotarbid arachnid *Palaeocharinus* (Fig. 3.4.5.4) of which several species have been described. The presence of book-lungs shows that these animals were truly terrestrial. The oldest known mites (*Protacarus*) occur in the chert and five species have been described. The earliest 'insect' *Rhyniella* also comes from the chert and is a collembolan or 'springtail'. Other fragmentary arthropod remains, named *Heterocrania* and originally assigned to eurypterids, are now considered to be of euthycarcinoid origin. In the Windyfield chert *Palaeocharinus*, *Lepidocaris*, *Heterocrania* centipede fragments, and a myriapod with gut contents including spores have been found recently.

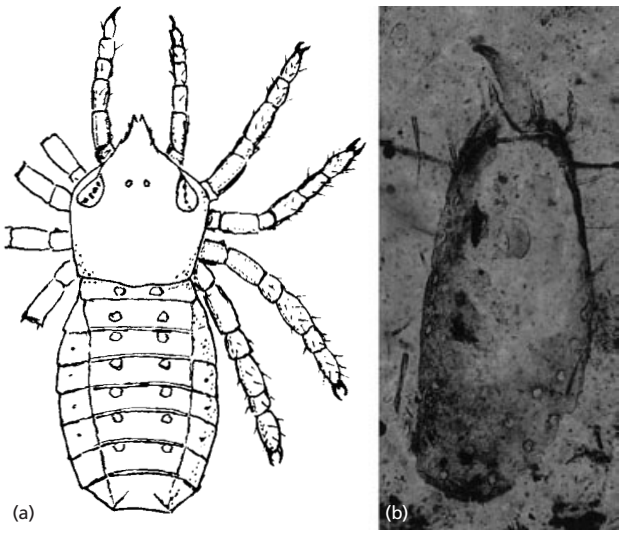

Fig. 3.4.5.4 The trigonotarbid *Palaeocharinus*. (a) Reconstruction from several sources, ×2.5. (b) Tarsus with claw preserved in chert, ×140.

The ecosystem

A variety of plant, animal, and fungal interactions have been demonstrated in studies of the Rhynie chert. The arthropods, dominated by carnivores (trigonotarbids, centipede), appear to belong to an early plant litter community (Edwards and Selden 1993). Decomposers (e.g. fungi) broke down the plants; detritivores (mites, collembolan, myriapod) fed on the degraded plant, fungal, and bacterial material, and were preyed on by the carnivores. Speculation centres on the degree to which the biota might have been adapted to the hot-spring conditions, and whether plant communities favouring specific conditions or substrates can be recognized.

References

Cleal, C.J. and Thomas, B.A. (1995) *Palaeozoic palaeobotany of Great Britain*. Geological Conservation Review Series no. 9. Joint Nature Conservation Committee, Peterborough.

Edwards, D. and Selden, P.A. (1993) The development of early terrestrial ecosystems. *Botanical Journal of Scotland* **46**, 337–366.

Kidston, R. and Lang, W.H. (1917–21) On Old Red Sandstone plants showing structure from the Rhynie chert bed,

Aberdeenshire. Parts I–V. *Transactions of the Royal Society of Edinburgh* **51**, 761–784; **52**, 603–627, 643–680, 831–854, 855–902.
Rice, C.M., Ashcroft, W.A., Batten, D.J. *et al*. (1995) A Devonian auriferous hot spring system, Rhynie, Scotland. *Journal of the Geological Society* **152**, 229–250.
Trewin, N.H. (1994) Depositional environment and preservation of biota in the Lower Devonian hot-springs of Rhynie, Aberdeenshire, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **84**, 433–442.
Trewin, N.H. (1996) The Rhynie cherts: an early Devonian ecosystem preserved by hydrothermal activity. In: G.R. Bock and J.A. Goode, eds. *Evolution of hydrothermal ecosystems of Earth (and Mars?)*, pp. 131–145. Proceedings of CIBA Foundation Symposium, no. 202. Wiley, Chichester.

3.4.6 Hunsrück Slate

R. RAISWELL, C. BARTELS and D.E.G. BRIGGS

Introduction

The Lower Devonian Hunsrück Slate fossils of western Germany are remarkable for two reasons: firstly because they represent the only fully marine Devonian Konservat-Lagerstätten that preserve extensive soft tissues, and secondly because they are pyritized. The diversity of the Hunsrück fauna provides a unique glimpse of marine life during the Devonian. Over 250 species of animal and 50 species of plant have been described (Bartels *et al.* 1998), but the importance of the Hunsrück Slate lies as much in the nature of the preservation as in the faunal diversity. The preservation of fine detail is particularly evident in X-radiographs (Fig. 3.4.6.1), which have played a pivotal role in developing interest in this deposit.

Soft-tissue pyritization is unusual in the fossil record, which is perhaps surprising in view of the ubiquitous occurrence of pyrite in fine-grained, organic carbon-bearing sediments. Apart from the Hunsrück Slate, extensive pyritization of soft tissue is known only in Beecher's Trilobite Bed (Ordovician, New York State) and at La Voulte-sur-Rhône (Middle Jurassic, south-east France) (see Section 3.4.7). The process of pyrite formation is mediated by sulphate-reducing bacteria which degrade organic matter and reduce dissolved sulphate to hydrogen sulphide. Decay normally results in the rapid loss of morphological detail. However, the unusual chemical features of the Hunsrück Slate allowed soft tissue to be replaced by pyrite before it was completely degraded. Although some detail has been lost (replication in apatite is faster and results in much higher fidelity), the Hunsrück fossils are greatly prized for their exquisite preservation (Fig. 3.4.6.2).

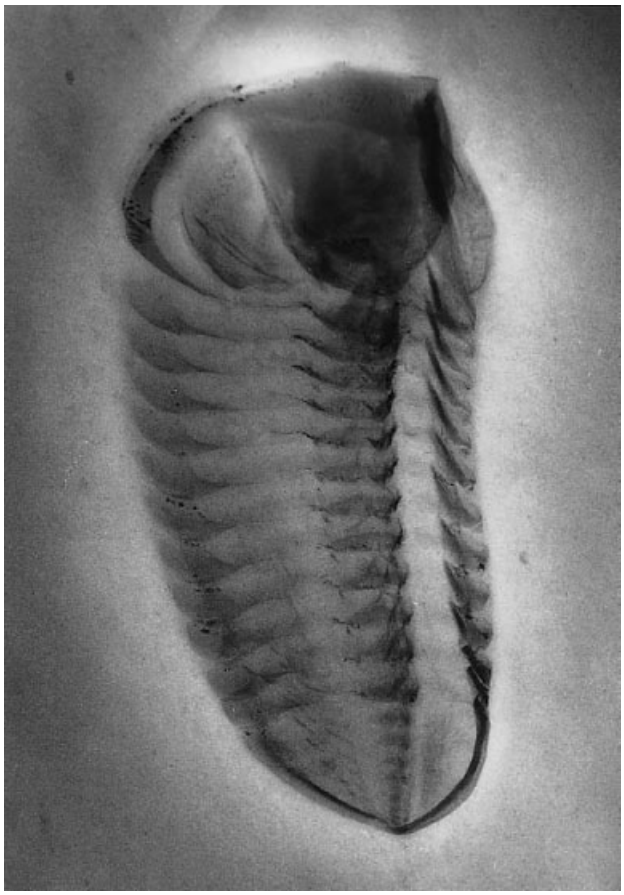

Fig. 3.4.6.1 Trilobite *Chotecops*, ×4; the *X*-radiograph shows how the right side of the exoskeleton is folded beneath itself, reflecting the oblique orientation to bedding; traces of pyritized appendages are evident at the rear on the left.

Sedimentary setting

The famous Hunsrück Slate Konservat-Lagerstätten around the village of Bundenbach belong to a sequence of clay-dominated sediments that occupies a NE–SW trending belt (approximately 140 km long by 15 km wide) lying mainly south of the Moselle and west of the Rhine. Sediment thickness varies from a maximum of 3750 m in the north-west to a minimum of ≈2300 m in the south-east. The main lithology is dark laminated mudstone, comprising interbedded clay and silt with some fine sand, including rare thicker lenses. The main minerals are chlorite (Fe-ripidolite), mica, quartz, calcite, and

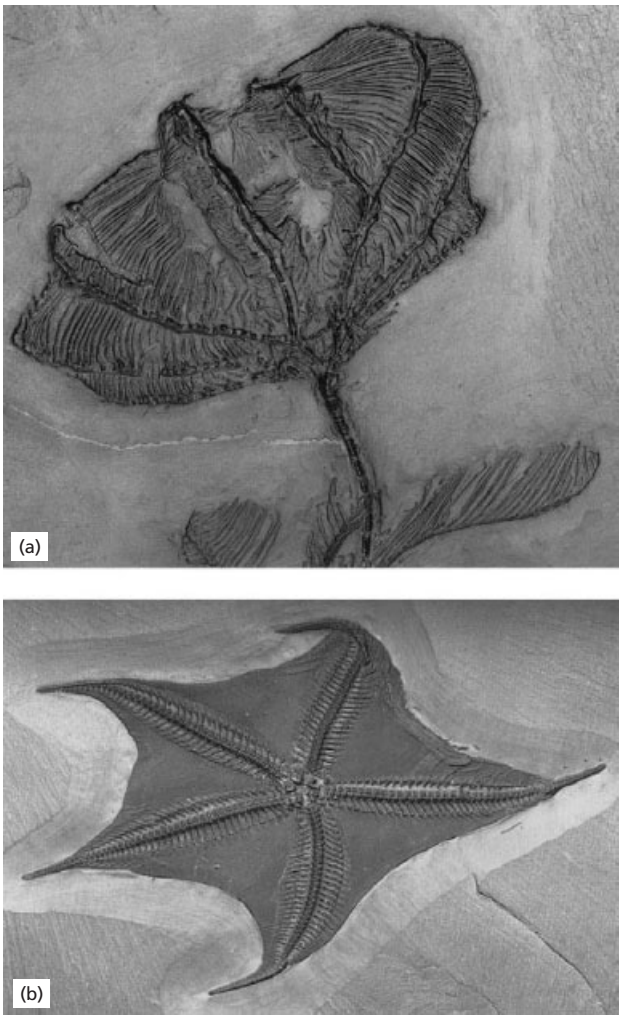

Fig. 3.4.6.2 (a) Crinoid *Hapalocrinus*, ×0.65. (b) Ophiuroid (brittle-star) *Loriolaster*, ×0.55; note the skin preserved between the arms, and wrinkled near their tips.

feldspar with smaller amounts of rutile, zircon, tourmaline, pyrite, and possibly some iron oxide. The slate-producing sequence around Bundenbach, which yields the pyritized fossils, is characterized by the occurrence of ubiquitous *Chondrites*, the trilobite *Chotecops ferdinandi*, and the goniatite *Anetoceras*. The presence of the dacryoconarid *Nowakia praecursor* defines its zonal position within the Lower Emsian. An abundant shelly fauna is limited to the sandy layers. Water depth in the depositional basin did not exceed 200 m, and decreased to the north-west and south-east as indicated by the absence of grading in the sands and the presence of bipolar crossbedding and lag deposits. The sediments were mobilized by storms and transported as low-density turbidites from shallow water to deeper areas below storm wave base. Subsequently, metamorphism to upper anchizone or lower greenschist facies resulted in the formation of slates with chlorite–mica porphyroblasts and a chlorite and mica groundmass. Slates have been extracted for roofing from approximately 1000 m of the sequence, particularly where cleavage and bedding coincide, which is also an important requirement for the preservation of the best fossils.

Deposition and preservation

The abundant laminations preserved in the Hunsrück Slate reflect low levels of infaunal activity. The most common burrows are open systems like *Chondrites*, which indicate that the substrate became relatively firm shortly after deposition. The burial of crinoids and sponges *in situ*, and the occurrence of numerous horizons preserving trails of trilobites and other arthropods, fish, and occasionally asteroids or ophiuroids, provide evidence that the overlying water was oxygenated. This is reflected in low values for degree of pyritization (typically <0.2). Most Hunsrück Slate localities yield disarticulated skeletons and soft parts are not preserved. The best-preserved fossils occur in areas of limited lateral extent, irregularly distributed through the slate-producing sequence at Bundenbach. Although many of the organisms were buried *in situ*, others, particularly the vagile forms, were transported over short distances to lower-lying areas of the sea floor. The turbidity currents resulted in burial in a variety of orientations to bedding. Rapid setting of the clay-rich sediment eliminated most scavengers and was the first critical step in preservation (Sutcliffe *et al.* 1999).

Extensive pyritization of the fossils (Briggs *et al.* 1996) is confined to the Bundenbach, Gemünden, and Breitenthal areas. Skeletons are either covered with a thin veneer of pyrite, or replaced by fine crystals (<20 μm), and occasionally framboids or larger euhedra. The appendages of trilobites (Fig. 3.4.6.1) and other arthropods are preserved as an infill of pyrite that precipitated within the exoskeleton after the muscle decayed, but before the limbs collapsed and the cuticle degraded. In some horizons the fossils are associated with phosphatic material, but soft-tissue preservation has not yet been reported from these examples.

The process of microbial pyrite formation begins with the breakdown of organic matter (represented as CH_2O below) to dissolved carbonate, accompanied by the reduction of sulphate to dissolved sulphide under anaerobic conditions:

$$2CH_2O + SO_4^{2-} \rightarrow 2HCO_3^- + H_2S$$

Dissolved sulphide then either reacts directly with iron oxides in the sediment, or with dissolved iron produced by microbial or abiotic reduction of iron oxides, to form

iron monosulphides with a composition approximating to FeS:

$$Fe^{2+} + H_2S \rightarrow FeS + 2H^+$$

The final step in the conversion of FeS to pyrite (FeS_2) may involve reaction with more H_2S, or with partially oxidized sulphur species formed from H_2S where bioturbation introduces oxygen into the sediment. Formation of pyrite is relatively slow, but the precipitation of FeS occurs rapidly, typically as a fine-grained coating on available surfaces. It is this rapid precipitation of FeS that represents the crucial step in preservation.

The anaerobic conditions required by sulphate-reducing bacteria commonly occur beneath the sediment–water interface in organic C-bearing sediments. Sulphate is reduced most rapidly in association with labile organic matter, such as soft tissue, that breaks down readily. The extent to which FeS can form from the sulphide produced, however, is limited by the diffusion of dissolved iron from the surrounding sediments. At normal sea-water pH values, dissolved sulphide and dissolved iron combine readily, restricting the precipitation of FeS to a thin zone between the locus of sulphide generation (the decaying carcass) and iron (the surrounding sediments). The position of this zone depends on the relative concentrations of sulphide and iron, and generally lies toward the lower concentration source (Raiswell *et al*. 1993).

Thus although a carcass decaying rapidly as a result of sulphate reduction creates high concentrations of dissolved sulphide, FeS will only precipitate in the carcass itself when the surrounding sediments contain even higher concentrations of dissolved iron. Such unusual conditions occurred in the Hunsrück Slate because the high iron oxide content of the sediment promoted iron reduction, while the low organic C content (outside the buried organisms) inhibited sulphate reduction except in association with the decaying carcasses. This is the final critical step that enabled dissolved sulphide to be trapped, and localized the precipitation of FeS and formation of pyrite in the carcasses (Briggs *et al*. 1996).

Biota

The levels within the Hunsrück Slate that yield pyritized fossils (Konservat-Lagerstätten) preserve a very complete record of a muddy bottom benthic community living at a depth below normal wave base (Bartels *et al*. 1998). Most of the organisms are represented in a range of sizes, including juveniles. Sessile forms are dominated by crinoids (≈30 genera) and include sponges, corals, conulariids, and some bivalves, brachiopods, and bryozoans. The crinoids (Fig. 3.4.6.2a), which were filter feeders, colonized the sea floor either as individuals or sometimes in large clusters. Many are attached to shelly fragments, and display extensions of the stem (cirri), which were used for anchorage and support in the muddy bottom. Juveniles are frequently preserved attached to adults, in life position. The vagrant benthos consisted mainly of arthropods (phacopid trilobites are most abundant; Fig. 3.4.6.1), of which a number, including the giant pycnogonid (sea-spider) *Palaeoisopus*, were predators. The trackways of arthropods are abundant on the upper surface of turbidites showing that they recolonized the sea floor rapidly after sedimentation events. Asteroid and ophiuroid echinoderms (≈14 genera each) (Fig. 3.4.6.2b) were also common (particularly the ophiuroid *Furcaster*), and in some cases approached 50 cm in diameter. Unlike their modern counterparts, many were probably deposit feeders. Larger swimming organisms include orthocone cephalopods and fishes, the latter mainly with broad flat bodies adapted for living and feeding on the muddy bottom. The largest predators were arthrodires. Only fragments of the spines and armour are known from the Hunsrück Slate, but they indicate that these fishes may have reached lengths of 2 m.

The Hunsrück Slate differs from most other Konservat-Lagerstätten (e.g. Burgess Shale, Solnhofen Limestone) in that the fauna is preserved where the organisms lived, rather than as a result of transport to another setting. In addition, soft tissues remained intact long enough to allow mineralization in spite of an oxygenated water column and the presence of a burrowing macrofauna.

References

Bartels, C., Briggs, D.E.G. and Brassel, G. (1998) *The fossils of the Hunsrück Slate: marine life in the Devonian*. Cambridge University Press, Cambridge.

Briggs, D.E.G., Raiswell, R., Bottrell, S.H., Hatfield, D. and Bartels, C. (1996) Controls on the pyritization of exceptionally preserved fossils: an analysis of the Lower Devonian Hunsrück Slate of Germany. *American Journal of Science* **296**, 633–663.

Raiswell, R., Whaler, K., Dean, S., Coleman, M.L. and Briggs, D.E.G. (1993) A simple three-dimensional diffusion-plus-precipitation model applied to localized pyrite formation in framboids, fossils and detrital iron minerals. *Marine Geology* **113**, 89–100.

Sutcliffe, O.E., Briggs, D.E.G. and Bartels, C. (1999) Ichnological evidence for the environmental setting of the Fossil-Lagerstätten in the Devonian Hunsrück Slate, Germany. *Geology* **27**, 275–278.

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3.4.7 La Voulte-sur-Rhône

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Introduction

The Jurassic (lower Callovian) soft-bodied biota from near the town of La Voulte-sur-Rhône (Ardèche, France) is extremely diverse and abundant. It is known only from a series of small quarries along the Ravin des Mines at La Boissine. These quarries have yielded a number of remarkable fossils, including pycnogonids, enigmatic crustaceans called thylacocephalans, and the oldest recorded octopus. Many of the fossils are preserved fully three-dimensionally in calcite or siderite concretions; those in the sediment are normally partially flattened. The preservation style is unique and characterized by the replacement of soft tissues by a number of different minerals (Wilby *et al.* 1996).

Sedimentary environment and biota

The fauna is restricted to an 8-m thick sequence of pyritiferous silty mudstones. The sediments were deposited in an episodically stratified, distal (probably quite shallow), low-energy marine environment, and form part of a generally metalliferous sequence. The fauna comprises two very different elements. The first is allochthonous and was introduced by turbidity currents from bordering oxygenated areas. It is dominated by soft-bodied benthic and nektobenthic forms, including worms, mysid and decapod crustaceans, thylacocephalan crustaceans, pycnogonids, and coleoid cephalopods. These frequently occur on bedding planes in death assemblages (Fig. 3.4.7.1). Their deposition by turbid currents is consistent with the occurrence of thin layers of sediment between each of the arms of some of the cephalopods (Fig. 3.4.7.2a), and was a critical factor governing their rapid and exceptional preservation (Fig. 3.4.7.2b). There is no evidence that any of these animals survived transport, and none is scavenged. Allochthonous shelly benthos is rare and generally poorly preserved. Some shells are replaced by pyrite, but most are extensively recrystallized or preserved as moulds.

The second element of the fauna comprises very abundant pavements of the presumably pelagic posidoniid bivalve *Bositra buchi*. Every specimen is preserved articulated with its valves splayed open wide. These horizons correspond to the background anaerobic conditions. Short-lived dysaerobic events in which the sediment was temporarily inhabited are recorded by rare levels containing simple horizontal burrows. Articulated specimens of the ophiuroid *Ophiopinna elegans* are common throughout the entire sequence. These fossils are also considered to have been pelagic (Dietl and Mundlos 1972).

Fig. 3.4.7.1 Bedding-plane death assemblage consisting of the crustaceans *Coleia gigantea* and *Archeosolenocera straeleni*, a priapulid worm, and the squid *Rhomboteuthis* sp. (arrowed), ×0.2.

Diagenesis

Energy dispersive system (EDS) elemental maps of polished sections of the fossils indicate that their hard parts (e.g. bones) and soft tissues (e.g. cuticles and muscle fibres) are preserved in apatite, calcite, pyrite, and galena. These minerals occur in a general diagenetic sequence in which successive phases replaced and/or coated earlier ones. Each diagenetic step resulted in a loss of anatomical detail.

Apatite was the first mineral to precipitate and is largely restricted to labile soft tissues such as muscle. Most of the muscle fibres are well preserved and are pseudomorphed quite precisely by phosphatized microbes. In extreme cases, however, only the external surfaces of the fibres were colonized by the microbes, and they are preserved as delicate external moulds (Fig. 3.4.7.2c). Other blocks of muscle are only very lightly phosphatized, and display centripetal gradients in the density of phosphatization, from a high at their periphery to a low at their centre. This implies that the source of phosphorus was external to the muscle. Phosphatization is known to be an extremely rapid postmortem process (Briggs and Kear 1994), and at La Voulte it stabilized the soft tissues for replacement by subsequent minerals.

Calcite precipitation postdated phosphatization, and was contemporaneous with and followed the earliest phases of pyritization. Calcite occurs predominantly as a non-displacive cavity-fill cement and occupies the interstices of soft tissues that are either coated by, or lightly

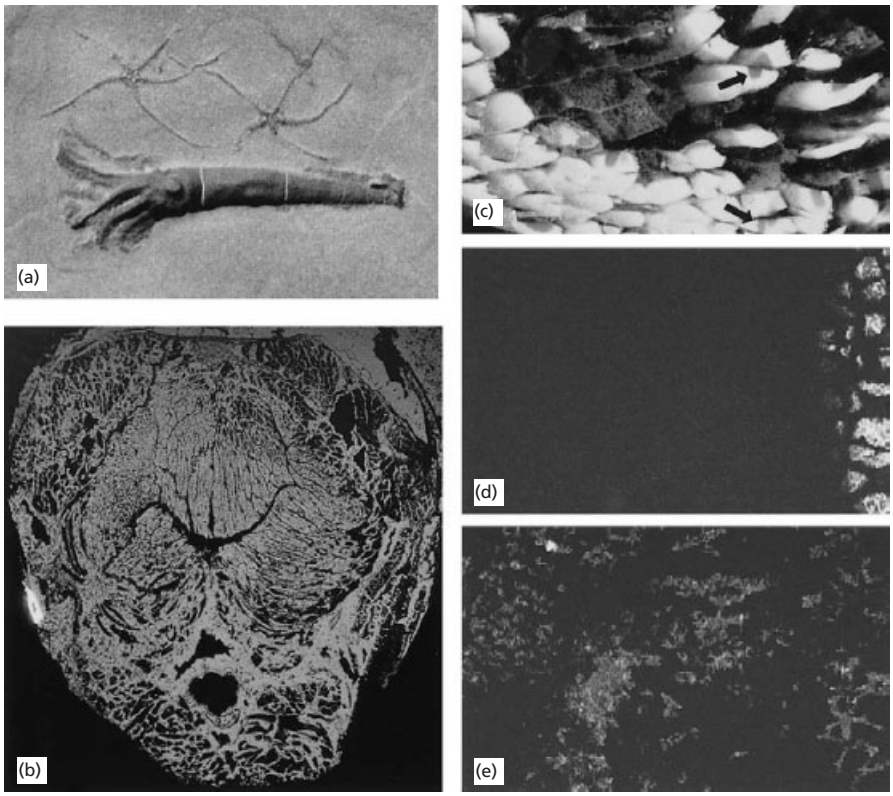

Fig. 3.4.7.2 (a) Three-dimensional pyritized squid *Rhomboteuthis lehmani* and articulated ophiuroids *Ophiopinna elegans*, ×0.33. (b–e) Transverse sections of fossilized soft tissues. (b) Three-dimensionally preserved decapod crustacean; most of the soft tissues, particularly the muscle fibres towards the periphery, are replaced by apatite (dark lozenges) and coated by pyrite (light reticulate areas); some fibres are pseudomorphed by pyrite (centre); calcite fills the interstices, ×10. (c) Phosphatized muscle fibres in the thylacocephalan *Dollocaris ingens*; densely phosphatized fibres (white blocks) surround other fibres (centre) that are lightly phosphatized and preserved as thin external moulds; some fibres are partially replaced by euhedral ferroan calcites (arrowed), ×33. (d,e) Phosphorus (apatite) and iron (pyrite) EDS elemental maps for a single field of view in *Dollocaris ingens*; variations in shade correspond to high (light areas) and low (dark areas) concentrations of the mapped element. (d) Densely phosphatized thick muscle fibres (right), ×30. (e) Phosphatized fibres seen in (d) are coated by pyrite; thin muscle fibres are either swamped by excess pyrite (centre) or replaced quite precisely (left); black areas are interstitial calcite, ×30.

mineralized in apatite and pyrite. In some fossils, the very earliest calcites are euhedral (<100 μm) and replace phosphatized soft tissues (Fig. 3.4.7.2c). This results in a substantial loss of the original tissue structure and, where extensive, results in its complete obliteration. In some thylacocephalans, very early calcite also occurs as distinctive crystal bundles (<1 mm). Identical structures have been described from other phosphatized biotas, and are known to have a microbial origin (Briggs and Kear 1994). They postdate phosphatization and are a response to a decay-induced rise in the pH of the carcass.

Pyrite is the most important mineral preserving the fish and plant specimens, as well as many of the squid (Fig. 3.4.7.2a) and crustaceans. It frequently replaces the gills, carapace, and hepato-pancreas of the crustaceans, and it coats and/or replaces initially phosphatized muscle fibres (Fig. 3.4.7.2b). The level of original detail that survives pyritization is dictated by its extent (Fig. 3.4.7.2d,e): too much and all detail becomes swamped; too little and only an indistinct mould is preserved. In some cases, a phosphate precursor to pyritization cannot be identified, but it is not clear whether this reflects direct pyritization of the soft tissues, or complete replacement of the apatite. Many of the fossils also contain large (often >1 cm), subspherical bodies of pyrite, and are surrounded by a halo of disseminated framboids. This implies that the locus of pyrite precipitation shifted during diagenesis from the carcass to the surrounding sediment. Similar haloes have been described from other pyritized biotas, and probably result from a shift in the position of the reaction front

between the iron derived from the sediment and the H_2S liberated in the carcass (Briggs *et al.* 1996).

Galena was the last of the major phases to mineralize the soft tissues. It predates the concretionary phases and some of the late cavity-fill calcites, and normally replaces earlier phosphatized soft tissues. Characteristically, it only preserves gross anatomical details.

The relationship of these minerals to one another provides clues to the processes of soft-tissue fossilization. Phosphatization was a prerequisite for the preservation of the fauna in other minerals. There is evidence to suggest that the diagenetic transformations were influenced by the type of taxon and tissue, and therefore occurred immediately postmortem. Each of the diagenetic steps was probably controlled by changes in the chemistry of the porewaters and of the decaying carcasses. Repeated shifts in the position of the redox boundary within the sediment may also have had an effect and were probably responsible for concentrating the metal ions.

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References

Briggs, D.E.G. and Kear, A.J. (1994) Decay and mineralization of shrimps. *Palaios* **9**, 431–456.

Briggs, D.E.G., Raiswell, R., Bottrell, S.H., Hatfield, D. and Bartels, C. (1996) Controls on the pyritization of exceptionally preserved fossils: an analysis of the Lower Devonian Hunsrück Slate of Germany. *American Journal of Science* **296**, 633–663.

Dietl, G. and Mundlos, R. (1972) Ökologie und Biostratinomie von *Ophiopinna elegans* (Ophiuroidea) aus dem Untercallovium von La Voulte (Südfrankreich). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **8**, 449–464.

Wilby, P.R., Briggs, D.E.G. and Riou, B. (1996) Mineralization of soft-bodied invertebrates in a Jurassic metalliferous deposit. *Geology* **24**, 847–850.

3.4.8 The Santana Formation

D.M. MARTILL

Introduction

The Santana Formation (?Albian, Lower Cretaceous) of the Araripe Basin, in north-east Brazil (Fig. 3.4.8.1), is famous for the abundance and high-fidelity preservation of its vertebrate and invertebrate fossils found within early diagenetic carbonate concretions. It is also an important source of pterosaurian skeletons with exceptionally well-preserved anatomical detail.

The Santana Formation comprises a diverse suite of sediments, including argillaceous red beds, green and grey clays, fine sands and silts, channel sandstones, and oil shales rich in phosphate. Thin conglomerates of catastrophic origin occur towards the base and include clasts from underlying sedimentary formations as well as the local metamorphic basement. A series of slightly silty clays with abundant carbonate concretions (with vertebrate fossils) known as the Romualdo Member occurs approximately midway through the sequence and represents a minor marine transgression into an otherwise fluvially dominated basin. The sequence rests disconformably on evaporites of the Ipubi Formation, and the whole is overlain by the largely arenaceous Arajara and Exu Formations in which mass flow and flash flood deposits are important (Fig. 3.4.8.1b). The thickness of the Santana Formation is variable (≈5–20 m), as is the assemblage of sediments, but the Romualdo Member with its characteristic concretions is present over the entire outcrop (Fig. 3.4.8.1a). The maximum thickness of the Romualdo Member occurs at the eastern and northern part of the outcrop where it may reach more than 10 m.

Palaeoenvironment

The Romualdo Member yields as many as 25 species of fishes, but turtles, crocodiles, pterosaurs, and dinosaurs are also present (Martill 1993). Invertebrates are less diverse but include the ostracod *Pattersoncypris micropapilosa* in superabundance, larvae of portunid crabs, small shrimp-like crustaceans, and molluscs (including corbulid bivalves and several small gastropods). Coprolites are very common and are often rich in small fish bone inclusions. Plants include horsetails, ferns, cycads, and indeterminate fragments of wood tissue.

The Romualdo Member was deposited in a shallow lagoon, which was probably connected with the open sea to the north-west, although evidence for this is largely circumstantial. Salinities probably fluctuated between brackish and hypersaline. At no time during deposition of the concretion-bearing horizon were normal marine salinity faunas present, but many of the fish taxa are also recorded from marine deposits elsewhere. Small echinoids are present in thin limestones just above the concretion-bearing strata, suggesting that near normal marine salinities were reached shortly after the concretion-bearing horizon was deposited. Seasonality of the environment is suggested by fine-scale laminations in the concretions; mass mortalities of the fishes may have been a consequence of seasonally fluctuating salinities, due either to dilution during rainy seasons or

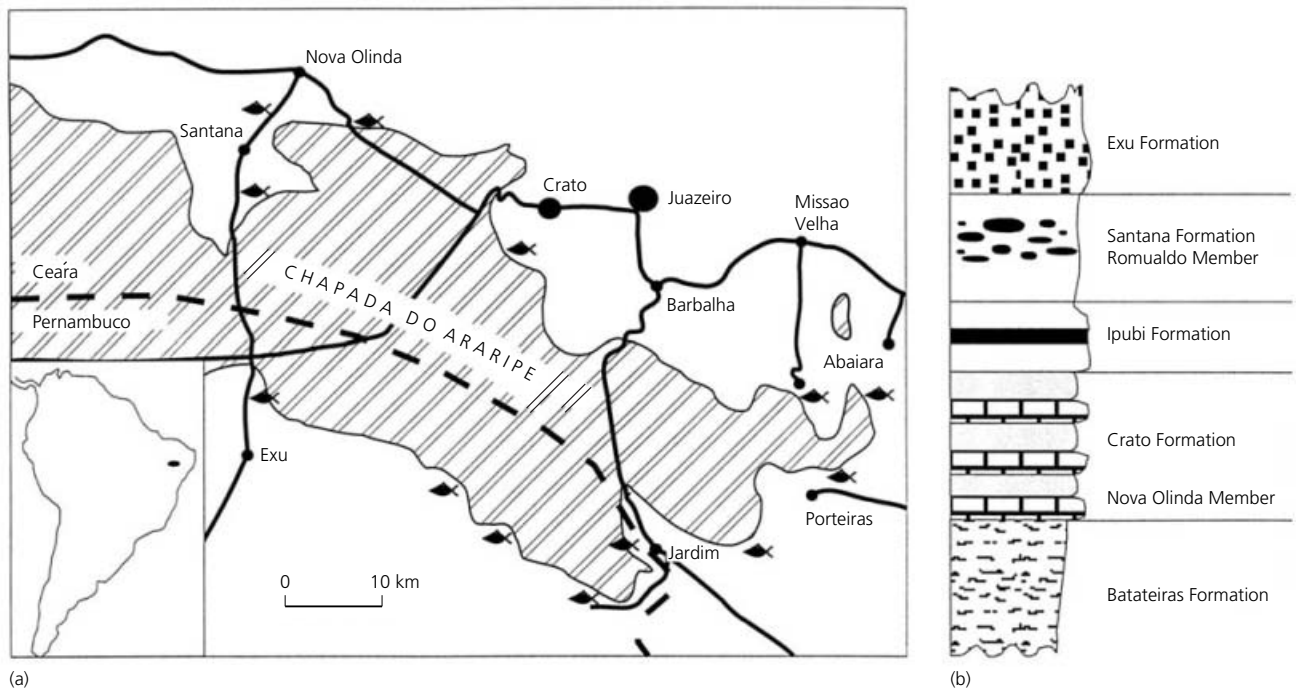

Fig. 3.4.8.1 (a) Chapada do Araripe, north-east Brazil, showing the outcrop of the Araripe Group and some of the important sites where fossil vertebrates are collected on a commercial basis. (b) Simplified stratigraphic section for the Araripe Group of the Araripe Basin; fossils with soft tissues are found in the Romualdo Member of the Santana Formation and the Nova Olinda Member of the Crato Formation. The thickness of the sequence varies, but the Santana Formation is ≈30 m.

perhaps evaporative hypersalinity of surface waters during prolonged dry seasons (Martill 1993).

Preservation

Vertebrate fossils are abundant and some of the fish species occur in mass mortality events represented by bedding planes covered with myriad small fishes. Many specimens are preserved three-dimensionally and retain body cavities. The skeletons may be fully articulated, although many show geopetal collapse following decay of soft tissues. Phosphatized soft tissues occur abundantly within both vertebrates and invertebrates in the concretions at many sites around the basin. They were first noted in ostracods with preserved appendages. Scanning electron microscopy of the soft tissues from fishes has revealed details preserved at the level of tissue, cell, organelle, and, more rarely, even at the macromolecular level; different decay states of the various tissues are also preserved (Martill 1998).

The soft tissues are preserved as metasomatic replacements by calcium phosphate. Commonly the phosphate occurs as subspherical aggregates, 1–3 μm in diameter, of crystallites in the size range 10–200 nm. Alternatively, individual phosphate crystallites appear to have nucleated on to specific sites in formerly proteinaceous and lipid-rich tissues. Occasionally the phosphate occurs as hollow, coalesced spheres, usually with a small opening bordered internally by a conical curtain; such structures are thought to represent autolithified bacteria that existed within the decaying carcasses.

A variety of soft tissues have been reported, including muscles, gill filaments, stomach and intestine linings, ovaries and ova, dermis, and blood vessels.

Preserved soft tissues have been reported from elopomorph fishes, particularly in *Rhacolepis* sp. and *Notelops* sp., where much of the body wall musculature and the gill filaments may be preserved (Figs 3.4.8.2 and 3.4.8.3). Many examples of the rare hybodont shark *Tribodus* show soft-tissue preservation, as does the batoid ray *Iansan*. Phosphatized tissues have also been reported in a pterosaur wing membrane, a small theropod dinosaur, and a crocodilian (Kellner 1996; Martill 1998). However, some taxa always lack preserved soft tissues, despite occurring abundantly and in the same concretions as species with soft tissues (e.g. the aspidorhynchiform fish *Vinctifer* sp.). This suggests that an aspect of the organism's physiology, or at least its decay chemistry, in part controls preservation.

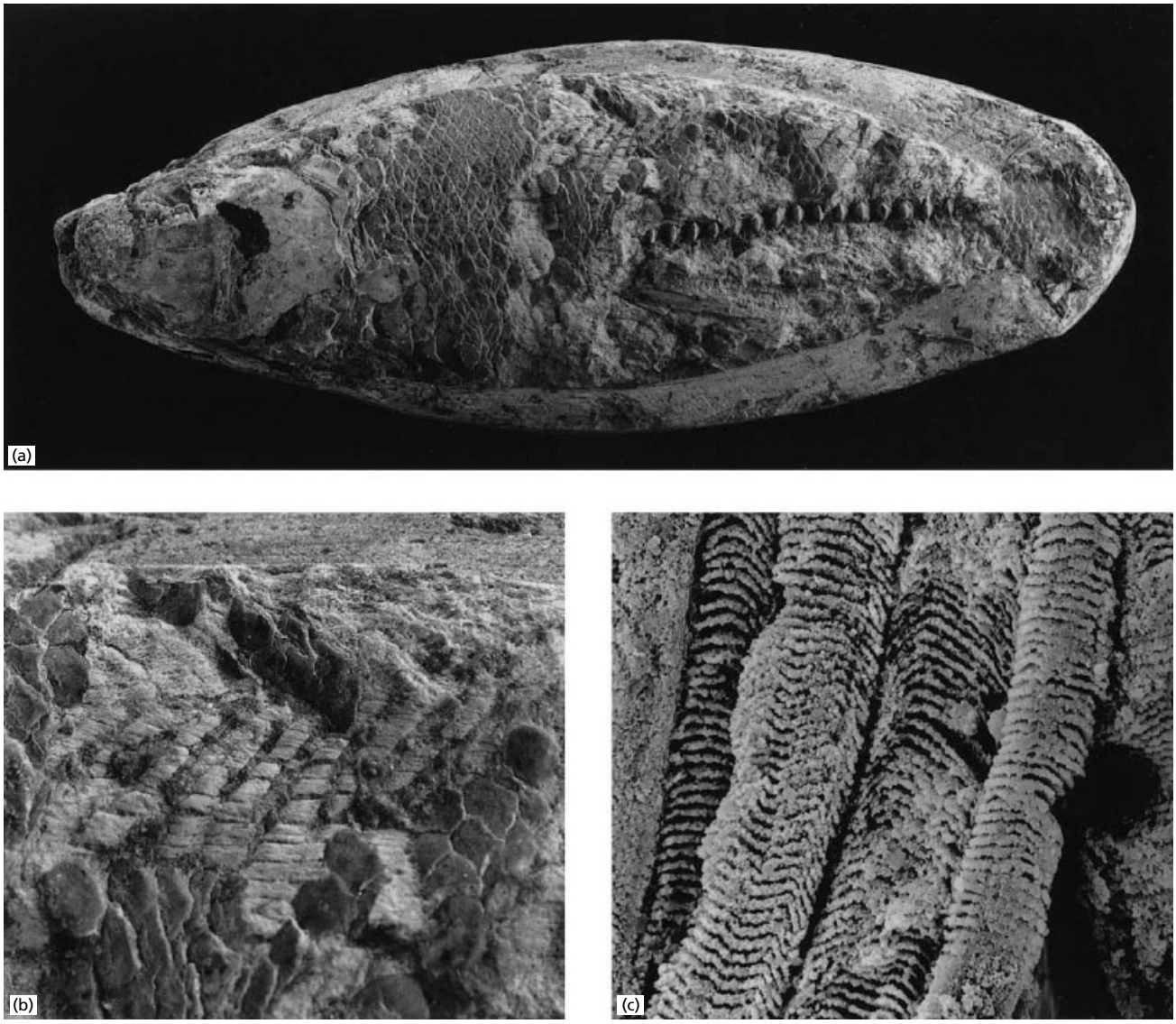

Fig. 3.4.8.2 Typical Santana Formation concretion from the Romualdo Member with fossil fish (cf. *Rhacolepis* sp.) showing phosphatized muscle tissues. (a) Complete fish, somewhat damaged during preparation, with muscle myomeres exposed in central portion of trunk, ×1. (b) Close-up of muscle myomeres showing preservation of fibres; there is evidence of break-up of the myomere blocks and separation of myotomes at the myoseptum due to decay prior to mineralization, ×3. (c) Scanning electron micrograph of muscle fibres showing banding typical of striated muscle, ≈ ×1300.

Timing of phosphatization

The high fidelity of preservation of soft tissues in fossils from the Santana Formation is an indication that replacement must have preceded, or at least accompanied, microbial decay, and was therefore a very early diagenetic event. Some of the fossilized soft tissues show morphologies which suggest that phosphatization accompanied decay. Tissues that appear to be partly decomposed occur alongside others that appear pristine (the *Medusa effect*; Martill 1989). Decay experiments reproduced features of the gill filaments seen in the fossil fish in a period of only a few hours to a few days. Laboratory experiments produced mineralized soft tissues in decaying shrimps after approximately 15 days which were remarkably similar to those in the Santana Fossils (Briggs *et al.* 1993).

After death many of the Santana fish sank like a dart into very soft sediment, where they are preserved at a high angle to the bedding. Such rapid burial suddenly

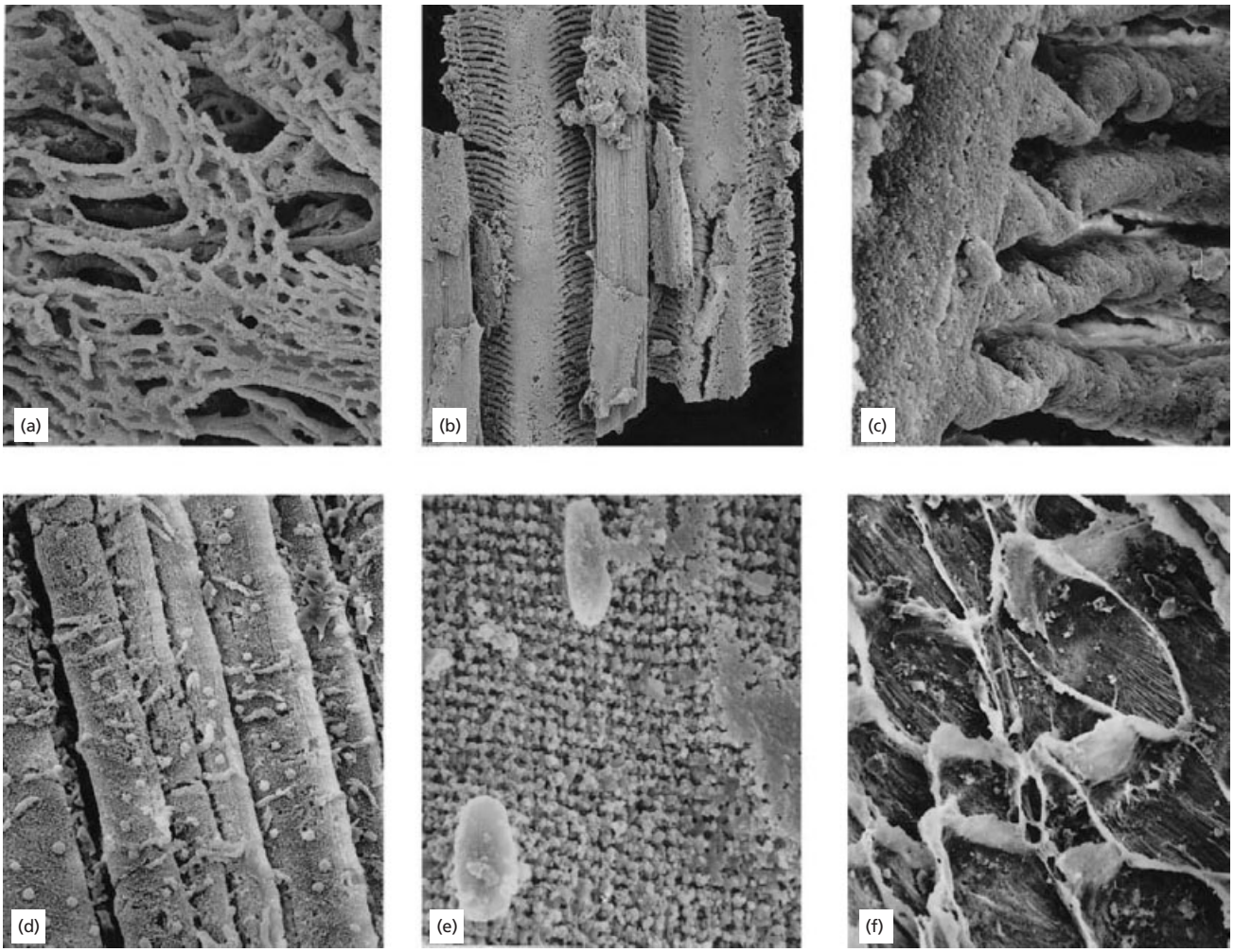

Fig. 3.4.8.3 Soft tissues replaced by calcium phosphate from elopomorph fishes (*Rhacolepis*, *Notelops*, and *Brannerion*) from the Santana Formation after preparation in 10% acetic acid. (a) Blood capillary network of gut wall, ×700. (b) Gill filaments with regularly spaced secondary lamellae and epithelial layer on surface of cartilaginous gill rays, ×70. (c) Afferent artery and basal part of secondary lamellae of gill filament showing slight collapse due to postmortem loss of blood pressure, ×1000. (d) Muscle fibres with T-tubules and ?nuclei, ×500. (e) Surface of single muscle fibre showing striations and oval bodies which may be nuclei or mitochondria, ×3000. (f) Myoseptum and lozenge-shaped outlines where sarcolemmic membranes of muscle fibres join myoseptum, ×200.

introduced the fish carcasses to diagenetic processes operating within the sediment. Microbial processes were fuelled by the carcass, resulting in the precipitation of calcium phosphate within the soft tissues and, perhaps simultaneously, the nucleation of calcite in and around the carcass to produce an early diagenetic, precompaction concretion. The phosphate nucleated on the soft tissues whatever their state of decay when they reached the bottom. Some fishes presumably sank immediately on death and arrived in near-perfect condition, whereas others may have floated for a period and partially decayed.

The source of phosphate for the fossilization of the soft tissues was largely external; the amount of soft tissue preserved in some individual specimens is too great for all the phosphate to have come from internal sources. Certainly, skeletal phosphate was not a source, because the skeletal elements themselves are in an exceptionally good state of preservation. Phosphate may have been derived from the decomposition of fishes killed during a mass mortality. Those species most sensitive to environmental change died early and their decay may have been well advanced before more tolerant species died. With the mass mortality of millions of individuals, phosphate levels could have risen steeply. In addition, toxification and attendant anoxia of the water column may have

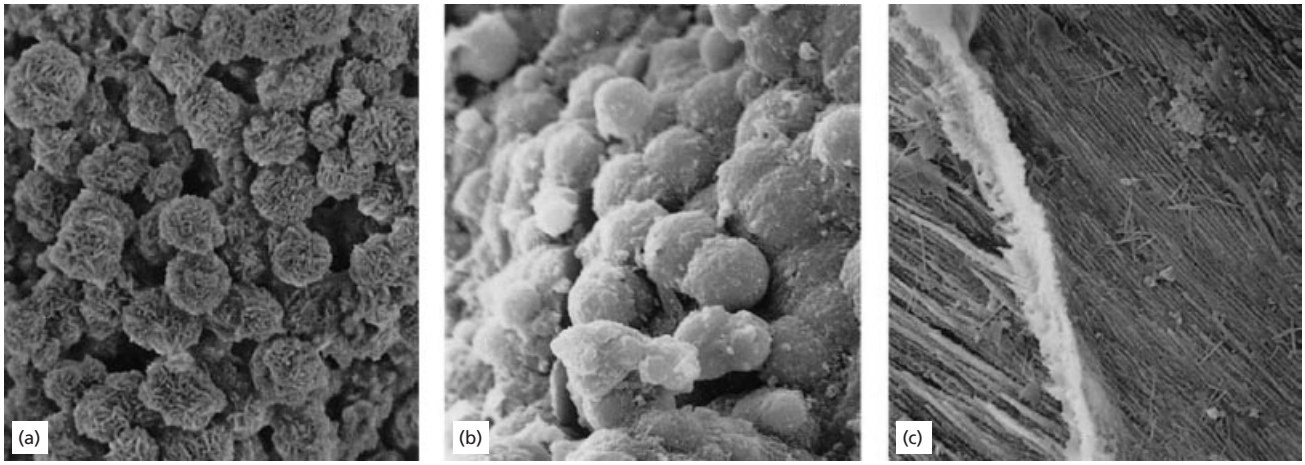

Fig. 3.4.8.4 Phosphate microfabrics in fossilized soft tissues. (a) Microspheres with cryptocrystalline apatite, ≈×20 000. (b) ?Autolithified coccoid bacteria, ×4000. (c) Templated crystallites in myoseptum, ×2000.

resulted in widespread collapse of the ecosystem. Phosphate liberated from early casualties would have been available for the preservation of those dying later. Such a scenario may in part explain the taxonomic bias seen in soft-tissue preservation.

Soft-tissue fidelity

Many of the phosphatized soft tissues in the Santana fossil biota are preserved with a high degree of fidelity. Muscle tissue of fishes may be preserved in their original myotomal blocks, showing clearly the V- or W-shaped arrangement along the body. Individual fibres may be seen, even with the naked eye. When viewed with the scanning electron microscope, muscle fibres may show the outer sarcolemmic membrane. Where the membrane is not preserved, the typical A- and Z-banding pattern of striated muscle is often present. T-tubules, mitochondria, and nuclei are also frequently preserved. In the most remarkable examples of preservation, myosepta preserved between muscle blocks often display collagen macrofibrils, while cells of the stomach wall retain their microvilli.

Although high-fidelity preservation is common, in other cases only the gross morphology of the tissue is preserved (Fig. 3.4.8.4). Differences in the fidelity of preservation are attributable in part to the morphology of the mineral habit of the calcium phosphate. The calcium phosphate usually precipitates as euhedral crystallites with lengths in the range 10–200 nm. When these template on to structural biopolymers such as proteins they produce faithful replicas of the tissue, often with preservation at the macromolecular level. However, the crystallites may be aggregated into microspheres with diameters of 1–3 μm (Fig. 3.4.8.4a). This latter habit does not allow high-fidelity preservation but can result in faithful replication at the cell level (Martill 1998). Even coarser levels of preservation occur where phosphatic autolithified bacteria replace the tissues (Fig. 3.4.8.4b), and only the gross morphology is evident. This habit is commonly seen in fish gill filaments.

Conclusions

The Romualdo Member of the Santana Formation ranks as one of the most important Mesozoic Fossil-Lagerstätten. Not only is it remarkable for the exceptional preservation of its fauna and flora, but the fossils are also highly abundant. The profusion of fish skeletons is partly a result of prolonged periods of soupy substrate maintenance in addition to the mass-mortality events. The Romualdo Member also contains one of the most diverse Cretaceous ichthyofaunas, and certainly the most diverse pterosaur assemblage known anywhere. The Santana Formation and the underlying Crato Formation (see Martill 1993), which yields abundant and diverse insects and plants, together provide the most comprehensive window on the Cretaceous life of Gondwanaland.

References

Briggs, D.E.G., Kear, A.J., Martill, D.M. and Wilby, P.R. (1993) Phosphatization of soft-tissues in experiments and fossils. *Journal of the Geological Society of London* **153**, 1035–1038.

Kellner, A.W.A. (1996) Fossilized theropod soft tissue. *Nature* **379**, 32.

Martill, D.M. (1989) The Medusa effect: instantaneous fossilization. *Geology Today* **5**, 201–205.

Martill, D.M. (1993) *Fossils of the Santana and Crato Formations, Brazil*. Field Guides to Fossils, no. 5. Palaeontological Association, London.
Martill, D.M. (1998) Resolution of the fossil record: The fidelity of preservation. In *The adequacy of the fossil record*, ed. S.K. Donovan, CRC Paul. pp. 55–74. London: Wiley.

3.4.9 Las Hoyas

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Introduction

The Las Hoyas basin is a small (50 km^2) half-graben which resulted from internal rifting of the Iberian Basin during the Early Cretaceous (Salas and Casas 1993). Located at the Serranía de Cuenca (east-central Spain; Fig. 3.4.9.1a), its deposits consist of 400 m of alluvial and lacustrine sediments belonging to the La Huérguina Limestone Formation (Upper Barremian). The palaeogeographical evolution of the basin was strongly controlled by tectonic activity, as evidenced by the depositional architecture of the sedimentary fill, and migrations of the depocentre. The climate was subtropical and semiarid, with alternating annual wet and dry seasons.

The Las Hoyas limestones have yielded a rich terrestrial and freshwater assemblage comprising more than 125 species and a similar number of genera. The organisms did not live where they were buried, but transport was short and gentle; at most they suffered nonturbulent transport from the shore and surrounding area towards the central part of the lake. Plants constitute 59% of the specimens but represent only 20% of generic diversity. Some 49% of the animal specimens are freshwater crustaceans. Vertebrate remains account for 18% of the animal specimens represented, of which just 0.1% are tetrapods.

The fossils are remarkable for their concentrated abundance and completeness. Decay-prone features are preserved as mineralized replications, or impressions. Evidence of skin, muscle tissues (retaining some three-dimensional details), glandular structures, and gut contents are preserved in some vertebrate specimens. Compound eyes, colour patterns of wings, antennae, and the ovipositors of certain insects have been reported. Also significant is the preservation of branchlets and fruiting bodies of charophytes, and articulated moults of belostomatid insects.

Sedimentary setting and depositional processes

The Las Hoyas biota occurs in a lacustrine, shallowing-upward sequence that consists of three major facies. At the base rhythmically laminated limestones represent sedimentation in a basinal lacustrine environment. Above this, thin-bedded and irregular slabby limestones were deposited in an intralittoral and sublittoral setting. Finally, at the top, crossbedded and massive limestones with brecciated tops and root traces correspond to the eulittoral realm (Fregenal-Martínez and Meléndez 1994).

Sedimentological analysis shows that this succession represents an extensive, perennial, shallow, alkaline lake system, with dysaerobic bottom conditions, which was fed by ground water and ephemeral storm-generated streams in a palustrine plain. The lake sediments are exclusively calcium carbonate, resulting from bio-induced precipitation, allochthonous influxes, and reworking of detrital particles. Microbial mats were developed on the lake bottom.

The fossiliferous laminated limestones consist of a rhythmic alternation of millimetre-thick dark and light laminae. Despite the apparent homogeneity of these limestones in the field, three microfacies have been distinguished, all the result of rapid sedimentation events. The first microfacies consists mainly of graded dark–light couplets, deposited as density flows and composed of detrital carbonate; it represents sedimentation under high lake-level conditions during rainy seasons. The second microfacies consists entirely of micrite which was deposited as dilute turbidites; it represents sedimentation under low lake-level conditions during dry seasons. The third, intermediate, microfacies is made up of alternating features of the other two, representing sedimentation during fluctuations in lake level. The stratigraphic and sedimentological evidence shows that the sedimentary evolution of the Las Hoyas lake was controlled by tectonics, climatic seasonality, and the provenance of the sediment.

Taphonomy

Two main taphofacies have been distinguished (Fig. 3.4.9.1b), reflecting contrasts in the composition and texture of the sediments, and in the depositional environment and diagenetic history.

Taphofacies 1 is characterized by sediment enriched in organic matter and clays (4–6%). The high concentration of organic matter apparently inhibited decay by creating a reducing acidic environment within which preservation of delicate and soft organic structures was promoted. It also favoured organic preservation, especially of plants. Disarticulation was linked mainly to the dissolution of bone in an acidic environment; the processes of infilling and cementation occurred at an

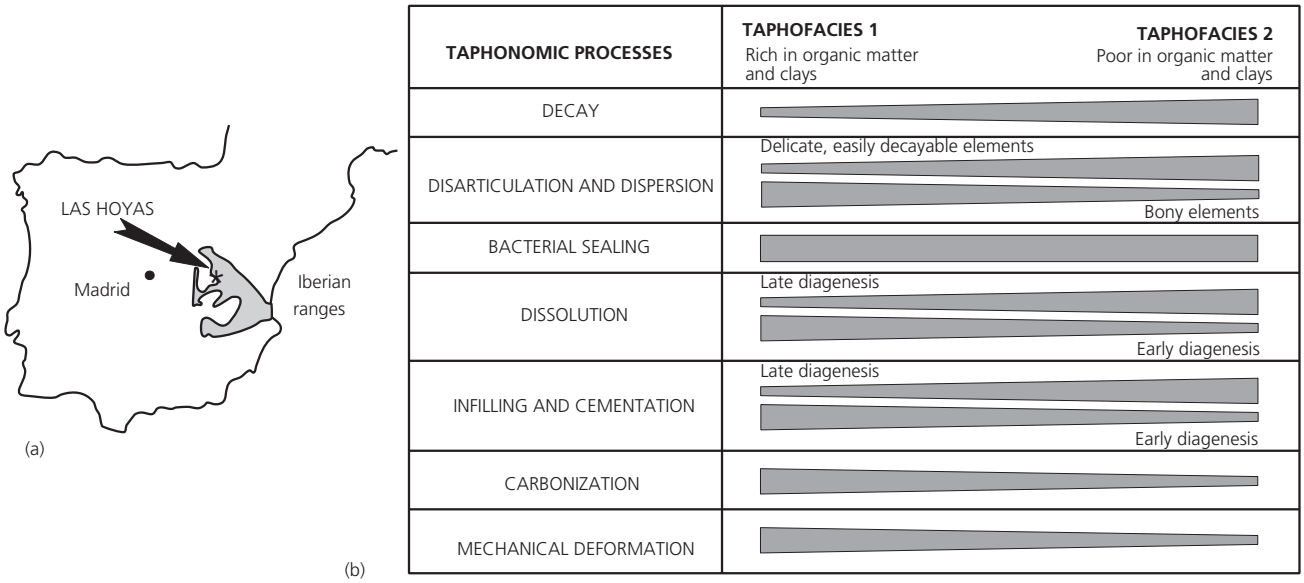

Fig. 3.4.9.1 (a) Location of the Las Hoyas fossil site. (b) Qualitative comparison of the development and gradients of variation of some taphonomic processes in the two taphofacies distinguished at Las Hoyas.

early diagenetic stage. The content of organic matter and clays favoured strong compaction and lithification of sediments, leading to deformation and flattening of specimens.

Taphofacies 2, in contrast, barely reaches 2% of organic matter and clays. Decay processes were more efficient and the preservation of delicate organic structures is mainly the result of sealing by microbial films. The sediments suffered less compression and the resulting rocks are more fissile. As a consequence, during regional alpine uplifting, meteoric waters circulated preferentially along lamination planes. This resulted in more dissolution and infilling of moulds than in Taphofacies 1.

Sedimentary dynamics are a major control on the taphonomic history of a deposit, just as depositional environment determines the composition and texture of sediments. In the case of Las Hoyas, a combination of bacterial mats, anoxia of the lake bottom, and rapid sedimentation explains most of the taphonomic features of the biota.

Biota

Most of the palynomorphs and plant macrofossils are characteristic of the European Wealden. Remarkably, however, the Las Hoyas flora is dominated by *Montsechia*, an enigmatic plant that accounts for up to 35% of the total specimens (flora and fauna). The floral diversity includes: charophytes (Clavatoraceae, Characeae, and Nitellaceae); bryophytes (*Hepaticites*); filicales (Schizeaceae, *Ruffordia*; Matoniaceae, *Weichselia*; Dicksoniaceae, *Onychiopsis*; and Osmundaceae, *Cladophlebis*); gymnosperms belonging to Bennettitales

Fig. 3.4.9.2 A basal centrocryptodiran turtle in ventral view. Scale bar = 10 mm. (Photograph by G.F. Kurtz.)

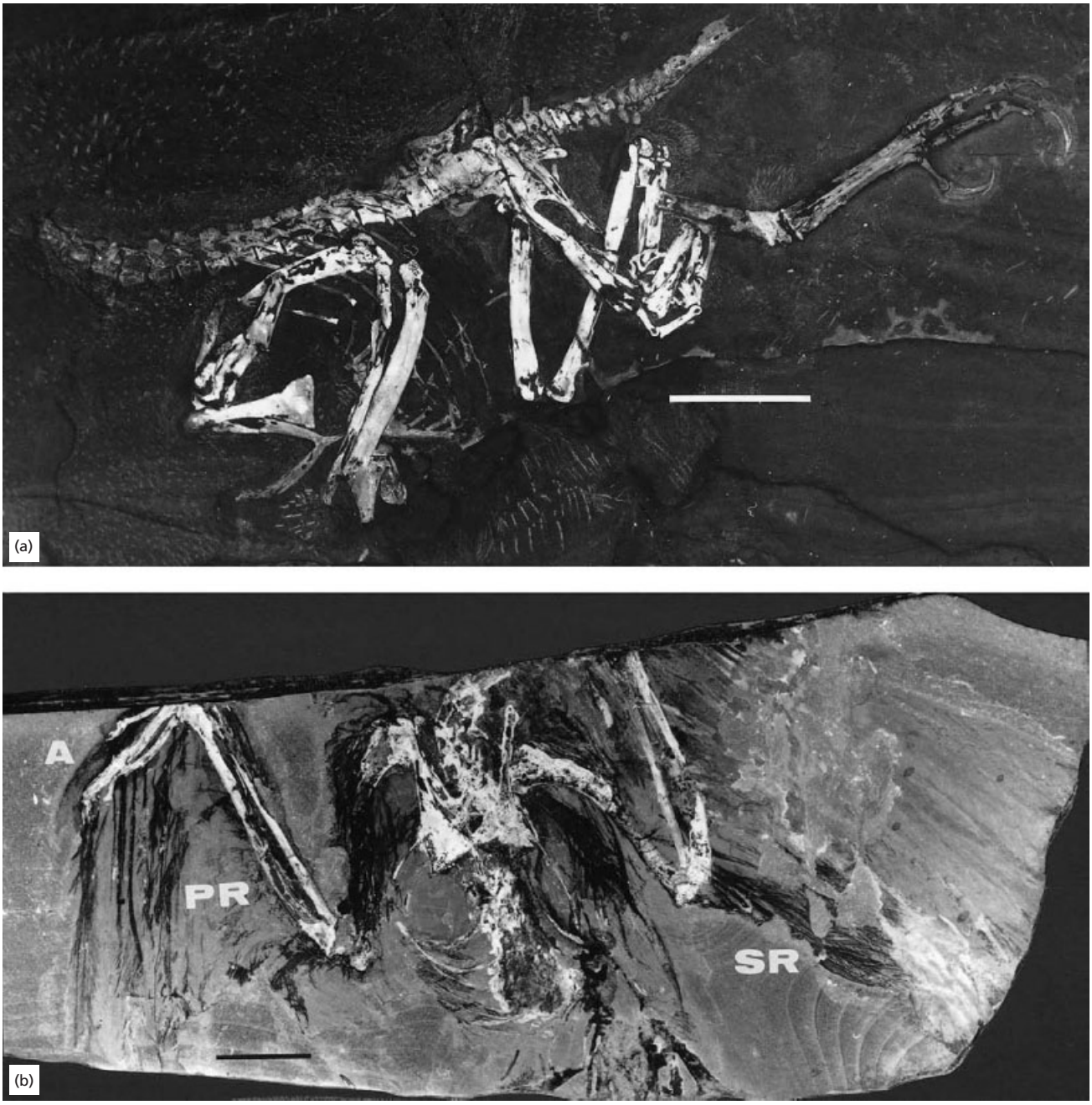

Fig. 3.4.9.3 (a) The primitive bird *Iberomesornis romerali*. (b) The enantiornithine bird *Eoalulavis hoyasi* before preparation: A, alula; PR, primary remiges; SR, secondary remiges. Scale bars = 10 mm. (UV-induced fluorescence photographs by G.F. Kurtz.)

(*Zamites*), Gnetales (*Drewria*), and Coniferales (*Cupressinocladus*, *Frenelopsis*, *Pagiophyllum*, *Brachyphyllum*, *Sphenolepis*, and *Podozamites*); and angiosperms (*Tricolpites* pollen, and isolated leaves).

The invertebrate fauna is composed mainly of arthropods (crustaceans, insects, and rare myriapods). Molluscs are rare (bivalves, ?Unionidae; and gastropods). The crustacean fauna comprises ostracods, peracarids (isopods and spelaeogriphaceans), and decapods (crayfish *Austropotamobius*; shrimp *Delclosia*). The insects include more than 35 species belonging to 14 orders. The Ephemeroptera (mayflies) is represented by Leptophlebiidae (*Huergoneta* and *Hispanoneta*). The Odonata (dragonflies) includes Aeschniidae (*Gigantoaeschnidium*, *Nannoaeschnidium*, and *Iberoaeschnidium*), Gomphidae (*Ilerdaegomphus*), and Aeshnidae (*Hoyaeschna*). The Blat-

todea (cockroaches) consists of mesoblattinids (*Nogeroblatta* and *Hispanoblatta*). The Isoptera (termites) includes the genus *Meiatermes* (among the earliest evidence for an insect worker caste). The Orthoptera is represented by crickets (Gryllidae, *Torcagryllus* and *Hoyagryllus*). Other rare orthopteroideans have been assigned to the genus *Chresmoda*. The Heteroptera is the most abundant insect group (Martínez-Delclòs *et al.* 1995), from which three belostomatid genera (*Hispanepa*, *Iberonepa*, and *Torcanepa*) have been described. The Homoptera is represented by Cixiidae. The sole specimen of Raphidioptera belongs to the Mesoraphiidae. The Coleoptera (beetles) includes Cupedidae, and some specimens provisionally identified as Ademosynidae and Scarabaeoidea. The Hymenoptera consists of a single specimen, probably belonging to the Apocrita. Specimens of Diptera (flies and mosquitoes) belong to the Nemestrinidae and the Stratiomyiidae. The Mecoptera (scorpion flies) are represented by the family Panorpidae. At least six different species of Neuroptera (lacewings) have been reported (Chrysopidae and Kalligrammatidae).

The waters of the lake were inhabited by at least 12 genera of bony fishes. The only sarcopterygian form has been provisionally assigned to *Holophagus*. Most of the fishes are actinopterygians: Amiiformes (amiids, *Vidalamia* and *Amiopsis*; and caturids, *Caturus*); Macrosemiidae (*Notagogus* and *Propterus*); Pycnodontiformes (*Macromesodon* and *Eomesodon*); Semionotiformes (*Lepidotes*); Pholidophoriformes (*Pleuropholis*); Ostariophysi (Gonorhynchiformes, *Rubiesichthys* and *Gordichthys*); and a diversity of at least four forms of primitive teleosteans whose phylogenetic relationships remain unresolved.

Three different amphibian lineages have been reported: the salamander-like Albanerpetontidae (*Celtedens*), Anura (the discoglossid *Eodiscoglossus*), and Caudata (*Valdotriton* and *Hylaeobatrachus*). The testudines (turtles) are represented by specimens of a unique unnamed member of the Centrocryptodira (Fig. 3.4.9.2). Several forms of lizard have been found, the best known being assigned to the scincomorph *Meyasaurus*. Crocodylomorphs are exemplified by forms ranging from advanced Crocodyliformes (close to *Lisboasaurus*) to Neosuchia (atoposaurids, *Theriosuchus* and *Montsechosuchus*; *Goniopholis, Unasuchus,* and an unnamed representative of the Eusuchia stem-group).

Perhaps the most famous Las Hoyas specimen is that of the theropod dinosaur *Pelecanimimus*. This primitive ornithomimosaur, of which only the anterior half of the skeleton is known, is characterized by the retention of many tiny teeth. The evidence of *Pelecanimimus* has resulted in a new hypothesis for the origin of toothless ornithomimosaurs (Pérez-Moreno *et al.* 1994). The edentulous condition was reached by miniaturizing the teeth and reducing their number. Three new bird genera have also been discovered at Las Hoyas: the basal ornithothoracine *Iberomesornis* (Fig. 3.4.9.3a), and the enantiornithines *Concornis* and *Eoalulavis* (Fig. 3.4.9.3b). These specimens have provided significant information on the early evolutionary history of birds and on the development of modern avian flight, i.e. birds with similar flying skills to modern forms appeared more than 100 myr ago (Sanz *et al.* 1996).

The Las Hoyas site yields a diversity of ichnofossils, produced by both invertebrates (*Cruziana*, *Helmintoidichnites*, *Palaeophycus*, *Lockeia*, and *Treptichnus*) and vertebrates (*Undichna, Pteraichnus*, and a trackway attributed to a *Goniopholis*-like crocodile). Fish coprolites are also abundant.

References

Fregenal-Martínez, M.A. and Meléndez, N. (1994) Sedimentological analysis of the Lower Cretaceous lithographic limestones of the Las Hoyas fossil site (Serranía de Cuenca, Iberian Range, Spain). *Geobios (Mémoire Spécial)* **16**, 185–193.

Martínez-Delclòs, X., Nel, A. and Popov, Y.A. (1995) Systematics and functional morphology of *Iberonepa romerali* n.gen. and sp. Belostomatidae from the Spanish Lower Cretaceous (Insecta, Heteroptera). *Journal of Paleontology* **69**, 496–508.

Pérez-Moreno, B.P., Sanz, J.L., Buscalioni, A.D., Moratalla, J.J., Ortega, F. and Rasskin-Gutman, D. (1994) A unique multitoothed ornithomimosaur dinosaur from the Lower Cretaceous of Spain. *Nature* **370**, 363–367.

Salas, R. and Casas, A. (1993) Mesozoic extensional tectonics, stratigraphic and crustal evolution during the Alpine cycle of the eastern Iberian basin. *Tectonophysics* **228**, 33–55.

Sanz, J.L., Chiappe, L.M., Pérez-Moreno, B.P., Buscalioni, A.D., Moratalla, J.J., Ortega, F. and Poyato-Ariza, F.J. (1996) An Early Cretaceous bird from Spain and its implications for the evolution of avian flight. *Nature* **382**, 442–445.

3.4.10 The Princeton Chert

R.A. STOCKEY

Introduction

The Princeton chert locality in British Columbia, Canada, has yielded one of the best preserved and most diverse Middle Eocene floras in the world. Fossils come from an outcrop of interbedded cherts and coals exposed along the east bank of the Similkameen River, a little over 8 km south-east of the town of Princeton, British Columbia. Fossils from this locality have been known since the late 1960s but received increasing attention from the

1980s onward. Fossil plant and animal remains are permineralized and preserved in three dimensions with internal cellular details that do not usually survive in fossil plant assemblages. This rare type of preservation has enabled detailed anatomical descriptions of several vascular plants and the reconstruction of whole plants from numerous isolated parts.

Depositional setting

The Princeton chert has been dated as Middle Eocene (48.7 Ma) using recent radiometric techniques. It forms part of the Allenby Formation of the Princeton Group, which has also been dated by palynology and the presence of diagnostic fossil mammals and fish. The outcrop records the changes in an aquatic plant community through 49 chert layers and interbedded coals (Fig. 3.4.10.1a). A few of the thinner chert layers grade into volcanic ashes across the outcrop. It is believed that the fossil plants and animals were infiltrated with silicic acid as a result of nearby volcanic activity. The low-lying basin received mineral-charged water that surrounded and infiltrated the plants and accumulated plant debris, where they grew, in a small lake or pond. Infiltration and hardening of the matrix was probably very rapid, as evidenced by the very fine preservation of the encased organic material. Such events were repeated at least 50 times at this site, where a subsiding basin enabled peat material to accumulate after each event.

The outcrop

The chert layers range in thickness from 1 to 55 cm, and while each is not unique in floral composition, certain trends are evident across the outcrop, with particular taxa such as *Metasequoia* disappearing in the upper layers, while pines and monocotyledons increase. There is a dramatic increase in ferns, especially *Dennstaedtiopsis* (Fig. 3.4.10.1b), after a large ash fall (layer 22); few flowering plants are present in these layers. Sampling into and across the outcrop has been attempted, but the data have not been analysed in detail.

Ecology

Evidence for the lacustrine nature of the Princeton chert deposits comes from several sources. A partially articulated skeleton and several isolated bones of *Amia*, a freshwater fish, have been reported from the shale overlying the plant beds (Wilson 1982). In addition, disarticulated remains of the fish *Amyzon* and *Libotonius*, and the remains of a soft-shelled turtle (Cevallos-Ferriz *et al.* 1991), further suggest this depositional setting. Fragments of turtle bones have been found in the chert itself, along with the fossilized plant material.

Aquatic plants

Many structural features of the plants indicate an aquatic habit. Aquatic adaptations include the presence of aerenchymatous tissues (parenchyma with air spaces), reduced vascular systems, and protoxylem lacunae. Aerenchymatous tissues provide for aeration and buoyancy (Fig. 3.4.10.1b). The submerged organs of living vascular plants show this type of tissue organization. Reduced vascular and mechanical tissues are very common in floating aquatic plants. The leaves of monocotyledons from the chert also show protoxylem lacunae or air spaces that lie adjacent to the vascular system and tracheary elements with little lignification.

In addition to structural features that indicate an aquatic habit, many of the flowering plants have affinities to extant aquatic plants. The Nymphaeaceae (water lilies), Lythraceae (loosestrife family), Alismataceae (water plantains), Cyperaceae/Juncaceae (sedges and rushes), and Araceae (aroids) are common in the chert (Pigg and Stockey 1996). Non-aquatic families such as the Vitaceae (grapes) are uncommon, and are only represented by a few seeds that were probably dropped into the basin via the guts of animals such as birds (Cevallos-Ferriz *et al.* 1991).

Evidence for *in situ* burial

Several plants were buried where they grew. *Eorhiza arnoldii* is the most common of these *in situ* plants (Fig. 3.4.10.1c,d). *Eorhiza* is an aquatic dicotyledon that bore strap-shaped monocotyledon-like leaves. Its stems (rhizomes), with attached and delicate branching roots, occur in growth position in the chert blocks (Fig. 3.4.10.1d). Extensive, branched rhizome systems up to 41 cm in length have been found with attached leaves, axillary branches, and roots, allowing the vegetative portions of this plant to be reconstructed (Fig. 3.4.10.1c). The probable reproductive parts have also been identified (Fig. 3.4.10.1e,f). Previously described as *Princetonia allenbyensis*, up to 13 of these flowers are now known to have been borne on an inflorescence (Fig. 3.4.10.1e); these can be linked to specific seeds, fruits (Fig. 3.4.10.1f), and pollen, making *Eorhiza* one of the best-known Eocene plants. The combination of characters that defines *Eorhiza* is unique, and this plant provides the basis of a new family of flowering plants.

Rare fossils

One of the most unusual features of the Princeton chert flora is the preservation of permineralized monocotyledons. Since these plants are usually herbaceous and often delicate, they are not usually preserved as fossils. Stems with attached leaves and roots are known

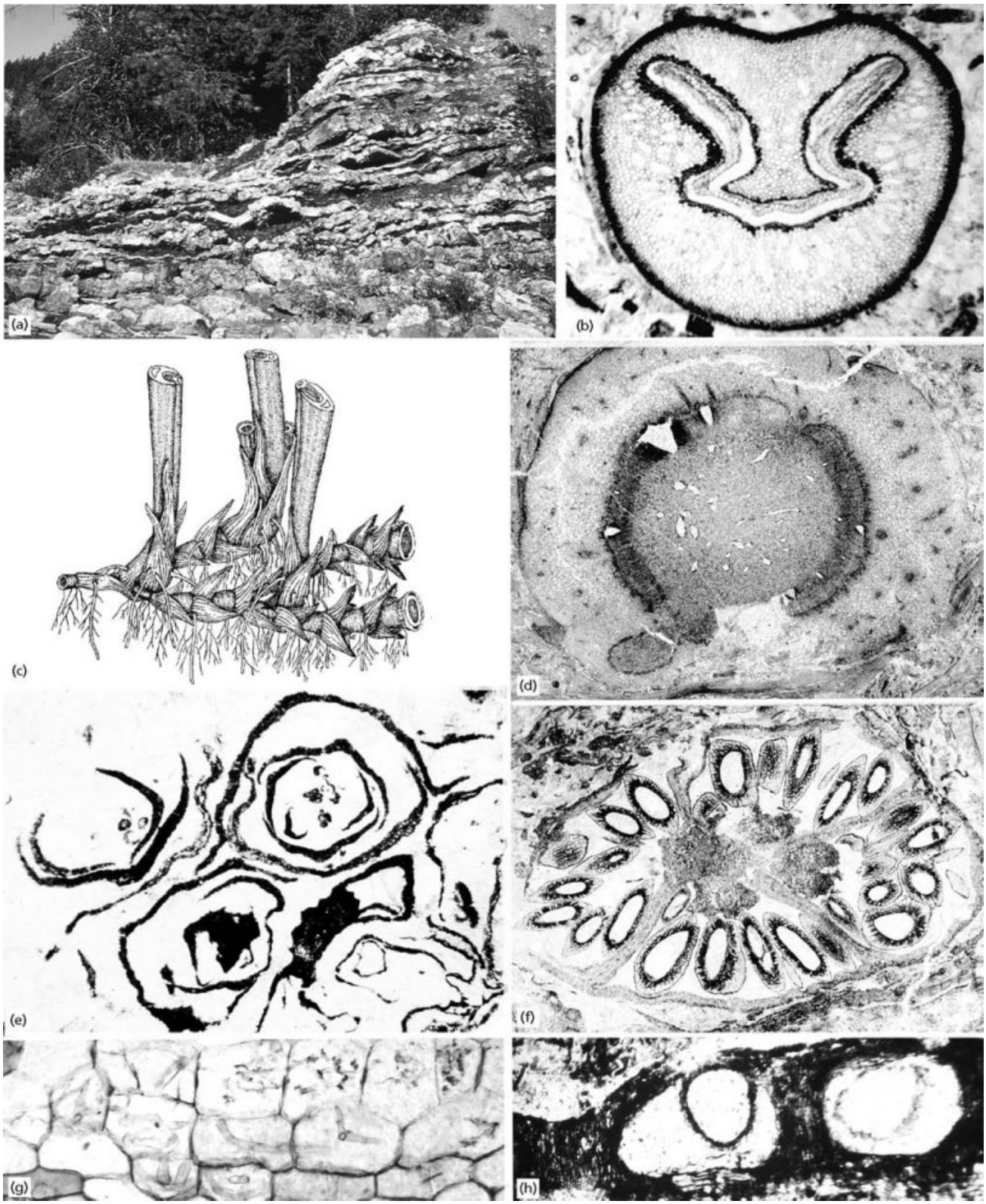

Fig. 3.4.10.1 Princeton chert. (a) Outcrop. (b) Cross-section of *Dennstaedtiopsis* petiole, ×12. (c) Reconstruction of *Eorhiza arnoldii*, ×0.1. (d) Cross-section of *Eorhiza* rhizome, ×1.4. (e) Cross-section of *Princetonia* inflorescence, ×22. (f) Cross-section of *Princetonia* fruit with seeds, ×9. (g) Mycorrhizal root of *Metasequoia milleri*; note the hyphae and arbuscules (top row) in cortical cells, ×280. (h) *Paleoserenomyces*, tar spot fungus in leaf of *Uhlia* palm; note the hyperparasite *Cryptodidymosphaerites* inside the locules of the tar spot fungus, ×70.

for *Ethela* (a sedge or rush) and *Soleredera* (Liliales). Other isolated plant parts are known, such as the fruits and seeds (with embryos) of *Keratosperma* (Araceae) and petioles of *Heleophyton* (Alismataceae). The best-known monocotyledon of the chert, and probably the most common in certain layers, is the palm *Uhlia*. This was a small coryphoid or fan palm that may have grown near the water's edge. Stems with attached petioles and roots, mid-ribs, and laminae are all known for these plants, which are good indicators of a subtropical climate.

Fossil fungi

As study of the vascular plants at Princeton progressed, many workers began to notice the presence of microscopic fungi on the leaves and in other plant organs. *Uhlia* palms have tar spot fungi associated with their leaves (Fig. 3.4.10.1h). These ascomycetes are now referred to as *Paleoserenomyces*; they were themselves being parasitized by the mycoparasite *Cryptodidymosphaerites* (Currah *et al.* 1998). This unusual case of a host plant with parasite that itself includes a mycoparasite has only been demonstrated once in the fossil record previously. The anthers of aponogetonaceous (primitive aquatic helobiaeoid monocotyledons) flowers from the Princeton chert have provided the first evidence of smut fungi in the fossil record. In addition to pathogenic fungi, the presence of both endomycorrhizal and ectomycorrhizal associations has been demonstrated. Roots of *Pinus* that are produced in coralloid masses with ectomycorrhizal associations are the first of this type demonstrated in the fossil record. Roots of *Metasequoia milleri* have recently been examined and compared to the vesicular/arbuscular mycorrhizae in living *Metasequoia* (Fig. 3.4.10.1g). Thus, mycorrhizal associations very similar to those in living taxa occurred at least 50 million years ago.

Conclusion

Ten fungi, four species of ferns, six conifers, 19 dicotyledons, and six monocotyledons have been described from this site. So far, all the evidence points to a freshwater lake or pond, periodically buried by nearby volcanics, regenerating vegetation, and repeated cycles of burial and preservation. Most of the preserved plants are aquatics and they probably grew in a subtropical climate.

References

Cevallos-Ferriz, S.R.S., Stockey, R.A. and Pigg, K.B. (1991) The Princeton chert: evidence for *in situ* aquatic plants. *Review of Palaeobotany and Palynology* **70**, 173–185.

Currah, R.S., Stockey, R.A. and LePage, B.A. (1998) An Eocene tar spot on a fossil palm and its fungal hyperparasite. *Mycologia* **90**, 667–673.

Pigg, K.B. and Stockey, R.A. (1996) The significance of the Princeton chert permineralized flora to the middle Eocene upland biota of the Okanogan Highlands. *Washington Geology* **24**, 32–36.

Wilson, M.V.H. (1982) A new species of *Amia* from the Middle Eocene of British Columbia. *Palaeontology* **25**, 413–424.

3.4.11 Dominican Amber

G.O. POINAR Jr

Introduction

Amber is a fossilized resin produced by both angiosperms and gymnosperms. When resin is no longer pliable, it falls into the general category of a copal. Over time and through the processes of oxidation and polymerization, the copal acquires the physical characteristics of amber. There are large deposits of copal around the world, especially in Colombia, South America, and these are often erroneously sold as amber.

Christopher Columbus appears to be the first European to have encountered amber from the Dominican Republic on the island of Hispaniola. Aside from its use as jewellery over the past few centuries, the amber attracted little attention until the mid-twentieth century, when its scientific value became apparent.

Depositional setting

Sixty-five million years ago, at approximately the same time that a giant meteor hit the Earth in the area now known as the Yucatan Peninsula in Mexico, solidified magma destined to become the island of Hispaniola emerged from the sea as part of the land mass known as the Proto-Greater Antilles stretching between North and South America, roughly where Central America exists today. Perhaps the two events were connected; the force of the meteor impact may have triggered earthquakes and volcanic eruptions that raised the ever-expanding magma above sea level. Global extinctions of many organisms, marine and terrestrial, at the end of the Cretaceous probably slowed the colonization of the Proto-Greater Antilles, but over time, life migrated to this island arc from the land masses to the north and south.

As the continental plate containing the Proto-Greater Antilles began to move slowly eastward into the Caribbean, it carried a menagerie of tropical life forms.

Vicariance biogeography thus played an important role in determining the range of fauna and flora that was present. Since its formation some 60–70 million years ago, Hispaniola has never been completely submerged (Donnelly 1992). Additional organisms arrived by passive or active dispersal over water (wind, floating debris, flight) or by temporary land bridges that formed during periods of low sea level as the plate continued to move and abut against terrain protruding from North America.

The plant that produced Dominican amber was *Hymenaea protera*, a representative of the Leguminosae. This now extinct species probably had an extensive range stretching from southern Mexico down to the Proto-Greater Antilles, across northern South America, and on to the still adjacent African continent. Interestingly, both morphology and DNA studies have revealed that *H. protera* was more closely related to the only species of *Hymenaea* remaining in East Africa than to the more numerous American species (Poinar 1991; Poinar *et al.* 1994).

The age of Dominican amber is still being debated. Different methods have indicated ages ranging from 15–20 Ma (on the basis of foraminiferans) to 30–45 Ma (by surveying coccoliths). Nuclear magnetic resonance spectroscopy has yielded ages ranging from 15 to 40 Ma. Further work is necessary to determine whether the amber now located in the Cordillera Septentrional of the Dominican Republic is the same age as that from the eastern part of the country. Certainly if *H. protera* existed during the early Tertiary, as evidence suggests, then amber production could have extended over a lengthy period.

Biota

Amber from the Dominican Republic has yielded the largest assemblage of fossils from any tropical site. Specimens so far identified include representatives of five kingdoms: Monera, Protista, Fungi, higher plants (Bryophyta, Pteridophyta, and Angiospermae) and 10 animal phyla (Protozoa, Nematoda, Nematomorpha, Rotifera, Mollusca, Annelida, Tardigrada, Onychophora, Arthropoda, and Vertebrata). Poinar and Poinar (1999) list 490 genera and 372 families of flora and fauna, as well as providing a reconstruction of the original forest. Among this huge assemblage are many taxa that are unique to these deposits, e.g. orchid bees, *Sphaerodactylus* lizards, and allantonematid nematode parasites.

Ecology and extinctions

The ability of resin to entrap organisms rapidly and retain them in pristine condition makes amber an excellent medium in which to study the past behaviour of life forms. Dominican amber has revealed rare fossil evidence of symbiotic animal–animal and animal–plant relationships. The former include predator–prey, parasite–host, and phoretic (one organism carried by another) associations. Figure 3.4.11.1a shows an ant and pseudoscorpion locked in mortal combat, with the mandibles of the ant clutching the pincer of the pseudoscorpion. Parasitic associations include mites with their mouthparts still inserted into the cuticle of insects, nematodes emerging from insects hosts, dryinid wasp larvae emerging from homopterans (Fig. 3.4.11.1b), strepsipterans (twisted wing parasites) hosted by fulgorids (planthoppers) and halictids (sweat bees), and, in one rare case, a group of first instar strepsipterans emerging from their mother's brood pouch while she still resides in a parasitized fulgorid. One of the rarest of all parasitic associations is the first definite fossil record

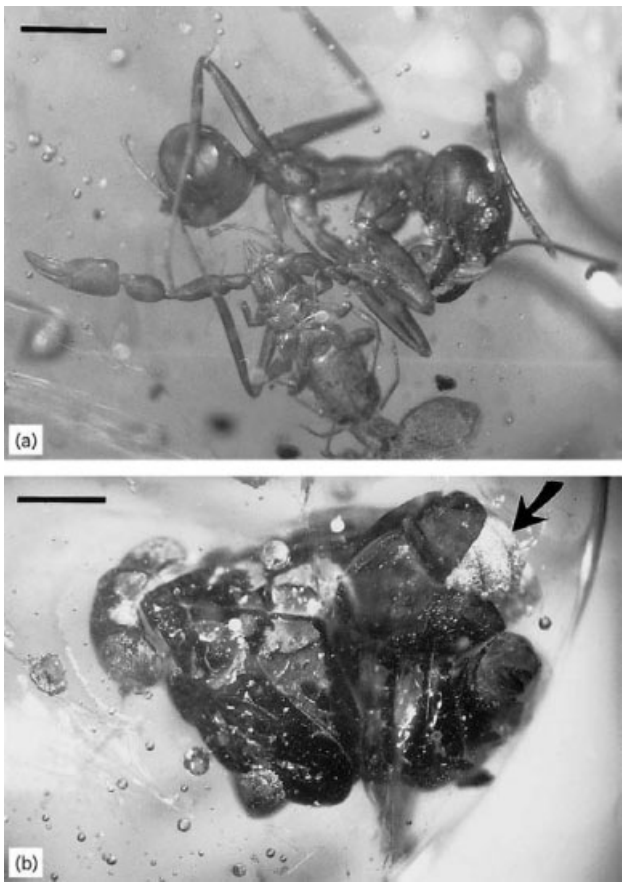

Fig. 3.4.11.1 Inclusions in Dominican amber. (a) An encounter between an ant (*Azteca alpha*: Formicidae: Hymenoptera) and a pseudoscorpion; the ant still clutches a pincer of the pseudoscorpion between its mandibles. (b) A mature dryinid wasp larva (arrow) (Dryinidae: Hymenoptera), which has just split open its larval sac, protruding from the abdomen of an issid planthopper (Issidae: Homoptera). Scale bars = 1 mm.

of adult Nematomorpha: a pair of hairworms emerging from a cockroach (Poinar and Poinar 1999).

It is obvious that one or more local extinctions occurred in the Caribbean that affected many plants and animals. Many groups found in Dominican amber are no longer present in Hispaniola, or even in the Greater Antilles, yet they occur in neighbouring South and Central America. Most of these genera are truly tropical forms which have little ability to survive under other conditions. It may be difficult to determine whether a genus is really extinct, as the biota of Hispaniola has not been completely catalogued. However, in the case of organisms such as bees, ants, and plants, which have been extensively studied, their absence can be confidently inferred.

The extinctions affected sufficiently many and varied groups to show that they are the result of natural phenomena, rather than due to human disturbance. Pathogens can be ruled out, since it is unlikely that diseases could have eliminated diverse groups of invertebrates and plants. Climatic changes offer a more plausible explanation for the disappearance of stenotopic tropical organisms (i.e. those able to survive only within narrow climatic parameters). The climate began to cool at the end of the Pliocene and this trend continued during the Pleistocene as a result of glacial activity and oceanographic changes associated with the closing of the Central American Isthmus. A mean drop of 4°C in surface water temperature in the Caribbean (causing extensive extinctions of marine molluscs and corals) (see Stanley 1987) would certainly have resulted in a drop in terrestrial temperatures throughout the Greater Antilles. Palaeoecological data based on fluctuations in plant distributions indicate that terrestrial temperatures fell 5–6°C in Panama and the Amazon basin, a drop that coincided with cooling over land and sea at all elevations in neotropical ecosystems (Colinvaux 1996). Truly tropical organisms never developed thermal homeostasis. When the cooling event occurred migration from Hispaniola was impossible and protective refuges were insufficient for survival. Both stenotopic plants and animals became extinct during this period and the loss of keystone species like stingless bees caused a cascade effect, resulting in the disappearance of predatory resin bugs, bee-dependent plants, and inquilines that lived in the bee colonies.

After the extinction events, when the climate again became tropical, reinvasion by organisms that had disappeared from Hispaniola but survived on the mainland of Central and South America presented difficulties. The prevailing winds in the Caribbean are from the northeast all year, providing little opportunity for air currents to carry organisms from any land mass to the Antilles. The absence of many tropical lineages from the Greater Antilles today supports the view that a significant portion of the original diversity was the result of a vicariant event rather than dispersal over water. The extinction event is difficult to recognize because the tropical climate was rapidly restored. It is only through a careful study of fossil assemblages that such an extinction event can be reconstructed. Clearly the evidence of the Dominican amber biota is critical to understanding the historical biogeography and palaeoclimatology of the Caribbean.

References

Colinvaux, P.A. (1996) Quaternary environmental history and forest diversity in the Neotropics. In: J.B.C. Jackson, A.F. Budd and A.G. Coates, eds. *Evolution and environment in tropical America*, pp. 359–405. University of Chicago Press, Chicago.

Donnelly, T.W. (1992) Geological setting and tectonic history of Mesoamerica. In: D. Quentero and A. Aiello, eds. *Insects of Panama and Mesoamerica*, pp. 1–13. Oxford University Press, Oxford.

Poinar, G.O. Jr (1991) *Hymenaea protera* sp. n. (Leguminosae, Caesalpinioideae) from Dominican amber has African affinities. *Experientia* **47**, 1075–1082.

Poinar, G.O. Jr and Poinar, R. (1999) *The Amber Forest*. Princeton University Press, Princeton, New Jersey.

Poinar, H.N., Cano, R.J. and Poinar, G.O. Jr (1994) DNA from an extinct plant. *Nature* **363**, 677.

Stanley, S.M. (1987) *Extinction*. Scientific American Library, New York.

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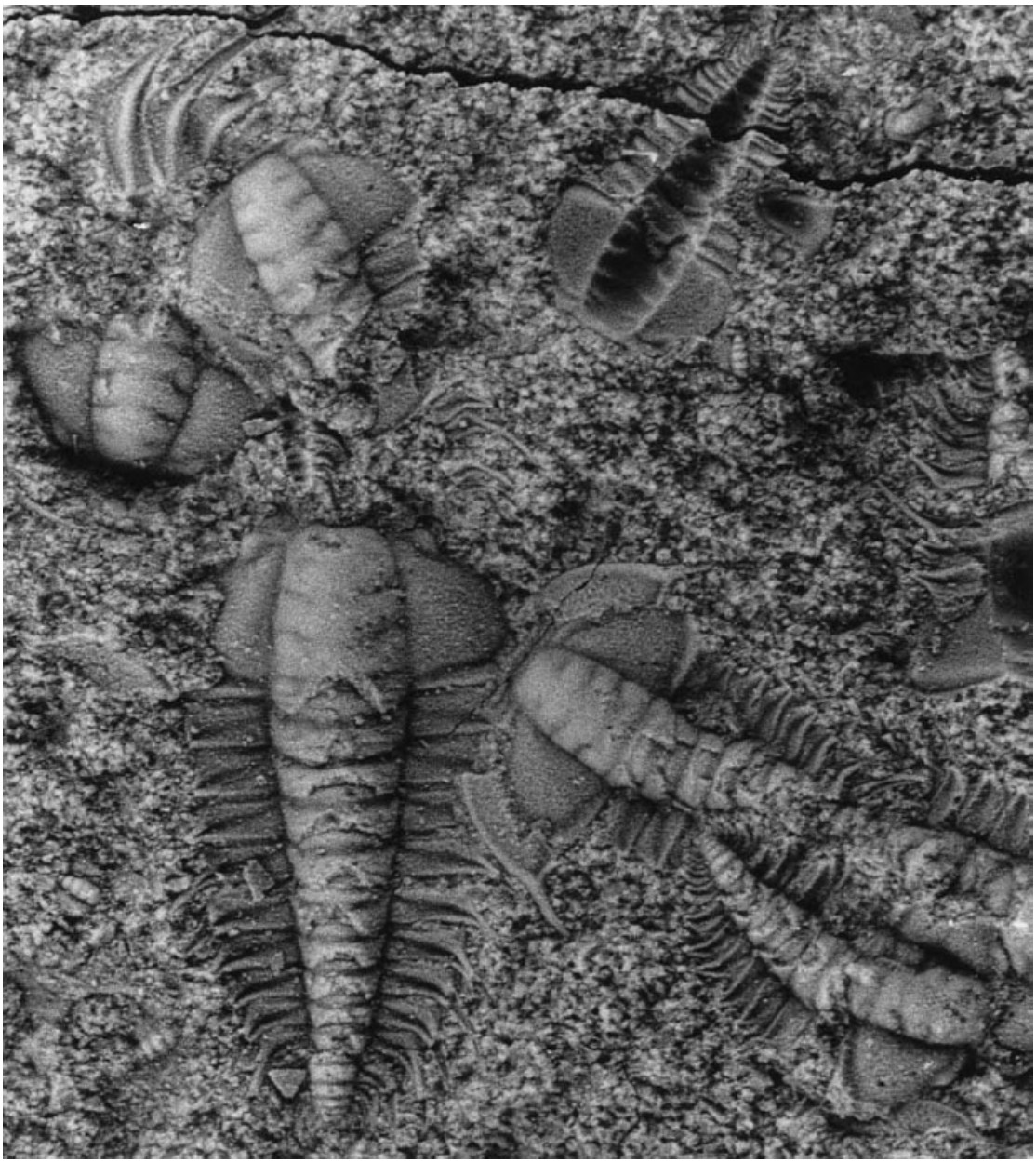

Larval stages (meraspides) of the olenid trilobite *Parabolina spinulosa* from the Upper Cambrian Alum Shales of Sweden, ×20. (Photograph courtesy of E.N.K. Clarkson, Edinburgh.)

4.1 Fossils as Living Organisms

4.1.1 Bringing Fossil Organisms to Life

P.W. SKELTON

Introduction

The French comparative anatomist Georges Cuvier (1769–1832) dazzled his contemporaries with his ability to conjure up the living forms and habits of extinct vertebrates from a few fossil bones or teeth. Lively images of dinosaurs and other monsters of the past have since become commonplaces of the screen and page. Yet the familiarity of such reconstructions belies the difficulties involved in making them. If imagination is not suitably disciplined, conclusions may go awry. In the nineteenth century, for example, geologists erroneously referred to many branching trace fossils as 'fucoids', because of their superficial similarity to seaweeds (Fig. 4.1.1.1).

The basis of both insights and errors alike was comparison, especially with living organisms. Cuvier's legendary skill depended on recognizing the characteristic components of known, functionally integrated, body plans. The misidentification of 'fucoids' also depended upon comparison, but at only a superficial level. With the development of the concept of trace fossils, it became apparent that burrow systems exhibited closer similarities than algal fronds. Thus the power of the comparative method, either to enlighten or to mislead, depends upon the depth of understanding of the models employed.

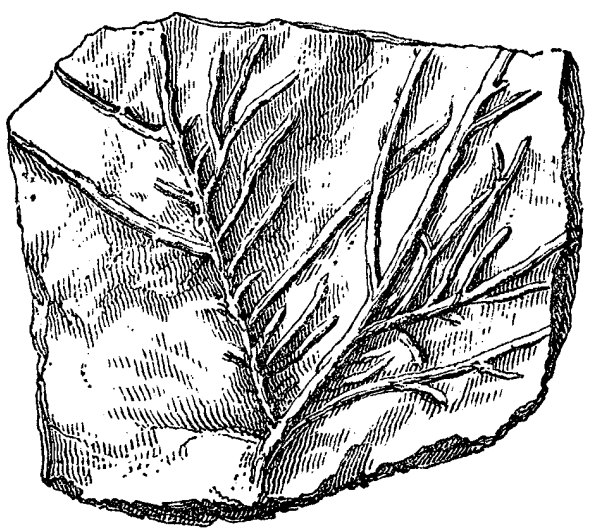

Fig. 4.1.1.1 A nineteenth-century reconstruction of 'fucoids', based on a branching burrow system, as illustrated by R.I. Murchison (1872) in *Siluria: a history of the oldest rocks in the British Isles and other countries . . .* , 5th edn.

'Bringing a fossil to life' has two aspects: (1) classification (what kind of organism?); and (2) inference of ecological attributes (how did it live?). Most body fossils yield sufficient information to allow taxonomic placement at some categorical level, but many aspects of the life habits of the organism in question may still remain obscure. Trace fossils frequently pose the opposite problem of providing clues to, say, the mode of locomotion or feeding, while their makers remain taxonomically anonymous. Chemical signatures of life (chemofossils) may fall either way, some being taxon-specific, while others testify to particular biochemical reactions that are nevertheless taxonomically widespread. For example, some of the oldest known rocks of sedimentary origin, from Isua in western Greenland (dated to around 3800 Ma), show a divergence in $^{13}C/^{12}C$ isotope ratios between the carbon in residual organic matter and that in carbonates (Schidlowski 1988). A similar (slightly greater) divergence is typical of younger marine deposits, and is widely regarded as a consequence of fractionation by autotrophic (largely photosynthetic) organisms, which preferentially assimilate the lighter isotope (^{12}C) during carbon fixation. Thus the isotopic evidence implies that autotrophic—if not photosynthetic—organisms were already in existence when the Isua rocks were deposited, although to which (presumably bacterial) groups they belonged remains unknown.

From fossils to organisms

It might be supposed that, since the issue of recognizing fossils as the remains or traces of organisms was already settled by the beginning of the eighteenth century, it scarcely merits mention today. The great bulk of the fossil record certainly no longer presents any problem in this respect. However, there still remain structures of questionable organic origin (dubiofossils), besides others that may look like fossils, but which probably had an inorganic origin (pseudofossils). Far from being curios on the sidelines of serious palaeobiology, such objects from Archaean deposits, in particular, command close attention, because many early life forms them-

selves only left fossils of rather simple form, not unlike inorganically produced structures. Criteria for distinguishing the fossils of simple prokaryotic cells from abiogenically produced carbonaceous spheroids, for example, are crucial if a reliable fossil record of first appearances is to be established. The debate about whether or not submicrometre-scale filamentous structures found in Martian meteorites represent primitive bacteria-like organisms further illustrates the point (see Section 1.1.2). Apart from sedimentary context (e.g. presence within stromatolites), one criterion used to diagnose simple spheroidal prokaryotes is a size distribution like that found in living populations (Fig. 4.1.1.2).

Reconstructing the form of organisms from their body fossils requires the 'thought-experiment' of reversing the intervening taphonomic history. The diversity of taphonomic influences is large, and the degree to which each has operated, and when, can vary greatly from one case to another, yielding a vast range of possible outcomes (see Section 3).

At best, in Konservat-Lagerstätten (see Section 3.4.1), factors promoting preservation (most commonly including rapid burial and early mineralization) have precluded destructive forces such as predation, scavenging, bioturbation, current reworking, and loss of material through decay and/or diagenetic disintegration. The resulting fossil, with a more or less intact skeleton, and possibly also evidence of the soft anatomy, places useful constraints on reconstruction of the original organism. Such fossils are especially valuable when they reveal the unfamiliar body plans of extinct taxa, for which no suitable comparisons can be found among living forms. An example is the discovery, in the Lower Carboniferous Granton Sandstones of Scotland, of exceptionally well-preserved examples of elongate soft-bodied animals bearing conodont elements—microscopic phosphatic tooth-like structures—in the head region (Briggs *et al.* 1983). Conodont elements had long been known to geologists, and indeed put to considerable stratigraphic service. Yet, until the Scottish discovery, the 'conodont animal' had remained notoriously enigmatic, and open to conjecture. Afterwards, it emerged as a rather distinctive kind of stem-group chordate. Instances of preservation like this are exceptional, however, and interpretation of more ordinary fossils may demand much detective-work.

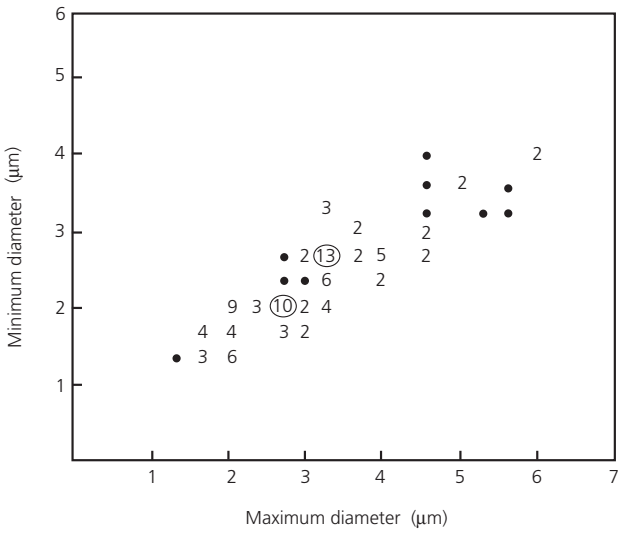

Fig. 4.1.1.2 Bivariate plot showing maximum and minimum diameters of some small spheroidal unicells (*Coniunctiophycus* sp.) found clustered in stromatolites of late Proterozoic age; numbers refer to multiple superimposed data points ($N = 102$). (Redrawn from Knoll and Calder 1983; with permission.)

The majority of body fossils represent only skeletal components, ranging from whole single shells to scattered or fragmentary remains. Attempts to reconstruct the original organism must then rely largely on reference to known body plans. Markings of soft-tissue insertion on the hard parts may provide valuable additional diagnostic clues. For instance, molluscan shells usually exhibit the sites of attachment of various body muscles. Prominent among these are insertions associated with retractor muscles from the animal's foot. In most shelled molluscs other than gastropods there are at least two pairs, sometimes more, of these pedal muscles. In gastropods, however, they became reduced to one pair, and thence effectively to a single muscle (in living taxa). This reduction seems to have been linked with the evolution of a remarkable stage in early gastropod development, called torsion, whereby the shell is rotated on top of the body, to become literally back-to-front. It is likely that torsion was itself a coadaptive adjustment to more compact, helical coiling of the shell. In consequence, the apex of the gastropod shell typically coils backwards (endogastrically), away from the animal's head. Evidence for multiple pedal muscle scars therefore offers a useful criterion for distinguishing the shells of non-torted univalved molluscs with a forwardly (exogastrically) coiled shell—monoplacophorans—from those of early gastropods (Fig. 4.1.1.3).

The problems of recognizing taxonomic affinities become especially acute with the scattered elements of multicomponent skeletons. Failing discovery of a complete and articulated skeleton, different assemblies may be conjectured. For example, the genus *Matthevia* is represented by conical shells, shaped somewhat like gnomes' hats, from stromatolitic carbonates in the Upper Cambrian of the USA. They were originally reconstructed as the bipartite shells of an extinct class of molluscs (Fig. 4.1.1.4a), dubbed Mattheva (Yochelson 1966). *Matthevia* associations were subsequently observed to comprise three distinct valve shapes, with identical

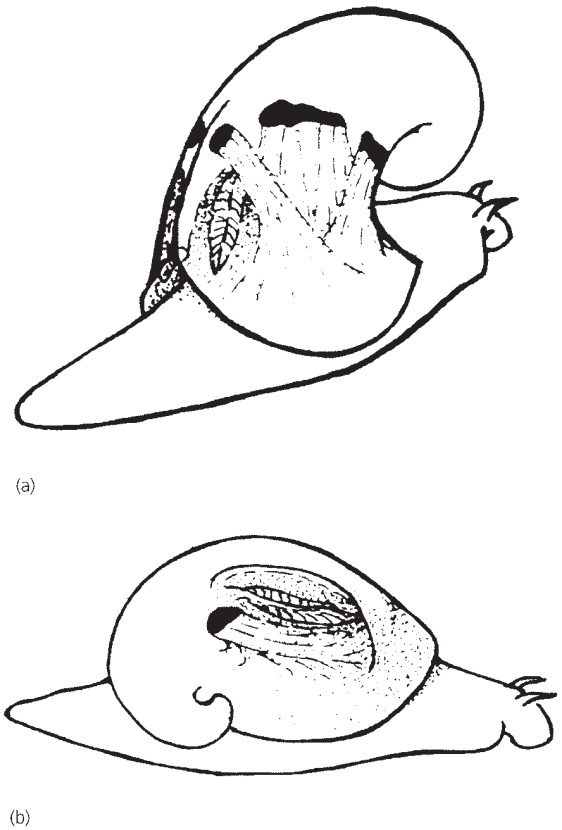

Fig. 4.1.1.3 Diagrammatic reconstructions of non-torted (a) and torted (b) univalved molluscs, showing pedal retractor muscles (insertions in shell shown in black), as well as gills within mantle cavity, inside shell. (a) Middle Devonian *Sinuitopsis*, identified as an exogastrically coiled monoplacophoran on the basis of multiple pedal muscle scars. (b) Upper Cambrian *Pelagiella*, a primitive gastropod exhibiting incipient helical coiling and a single pair of pedal retractor muscle scars (only one of which is shown here). (a, Based on Rollins and Batten 1968; b, based on Pojeta 1980.)

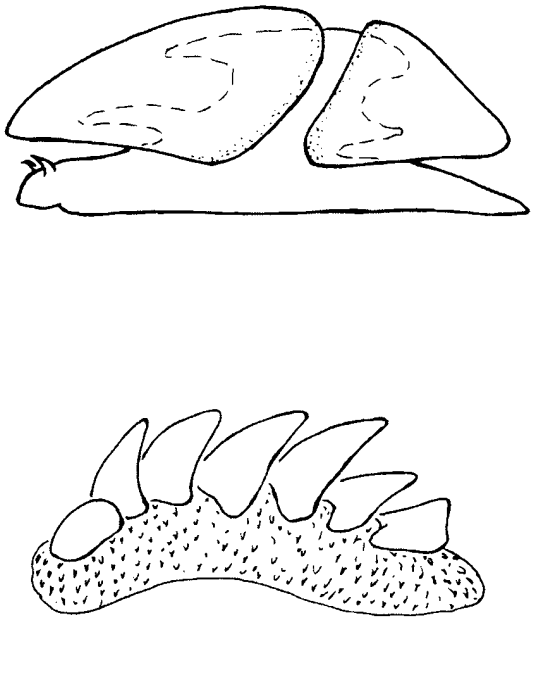

Fig. 4.1.1.4 Reconstructions of *Matthevia*: (a) as the bipartite shell in a presumed extinct class of molluscs; (b) as a chiton. (a, Based on Yochelson 1966; b, based on Runnegar *et al.* 1979.)

ornament, rendering the bipartite reconstruction unlikely. Similarities with the valves of an undoubted chiton of Ordovician age (*Chelodes*) revealed that *Matthevia* is the earliest known member of the existing Class Polyplacophora (Fig. 4.1.1.4b) (Runnegar *et al.* 1979). In this case, finding a home for the specimens in an extant taxon, and thus a guide to the likely body form of the original animal, involved detecting parallels with other, similar fossils of better understood taxonomic affinity.

Such an approach is doomed to failure, however, with scattered hard parts from members of an extinct taxon with an unfamiliar body plan. As with the conodont animal, enlightenment generally has to await the *deus ex machina* of a Konservat-Lagerstätte containing articulated specimens. Those who work on the Cambrian explosion of metazoans (see Section 1.2) often have to rely on such miracles of preservation, because of the abundance of taxa that flourished briefly before suffering extinction. Prior to the discovery of articulated specimens of the worm-like *Halkieria*, covered by an elaborate chain-mail coating of shelly sclerites (Conway Morris and Peel 1990) (see Section 1.2.2), the pattern of assembly of the isolated sclerites had been unclear, with no hint of the large flattish plates at either end of the body. This and many other such examples point to the immense importance of Konservat-Lagerstätten in palaeobiological reconstruction, especially for the older, more remote, fossil record of lost body plans.

From organisms to life habits

In trying to bring fossil organisms to life, the comparative method remains the main guide. But it is an ambivalent one because an organism's form is the product of evolutionary history as well as a response to prevailing circumstances. The imprint of history on form is strong because of the pervasive controls on development exerted by the inherited legacy of genes. The historical signals of form, if interpreted uncritically, may

prove misleading. As a banal illustration, it would not be sensible to infer that Siberian mammoths lived in a hot climate just because living elephants do. Their shared 'elephantness' is a historical signal of their common ancestry, not a reliable guide to climate. The thick shaggy coat in mammoths, on the other hand, more plausibly suggests a cold climate. How can the two kinds of signal be distinguished?

A useful perspective on the problem is to think of organisms as belonging simultaneously to two distinct hierarchies in the organization of nature (Eldredge 1985) (see Section 2.3.6). As members of local populations, they participate in the flow of matter and energy through communities and so on through ecosystems, i.e. in an ecological hierarchy. As products of evolution, they also belong to a genealogical hierarchy. While the ecological hierarchy refers to a dynamic web of interactions operating at any one time, the genealogical hierarchy concerns the nested sets of taxa that are the historical outcome of phylogeny. So the present quest is for those features of fossil organisms that reflect their place in the ecological hierarchy.

The phylogenetic component of form can best be revealed by cladistic analysis, which codifies the distribution of derived character states among organisms in a branching diagram, or cladogram (Fig. 4.1.1.5; see Section 5.3.1). In the most parsimonious arrangement of character states, it is assumed that a derived character state shared exclusively by the members of a given branch in the cladogram (e.g. character state *a'* in Fig. 4.1.1.5) has been inherited from a single common ancestor: the similarity is considered homological. Similar character states may have evolved independently in different taxa, however, as a consequence of adaptation to equivalent conditions. Such analogical similarities (e.g. character state *b'* in Fig. 4.1.1.5), lacking a common derivation, will tend to be separated on different branches of the cladogram. While the homological similarities between organisms represent the historical signals mentioned above, isolated analogical similarities reflect discrete adaptations. Cladistic analysis thus offers a means to distinguish the latter, often more ecologically informative signals, from the former.

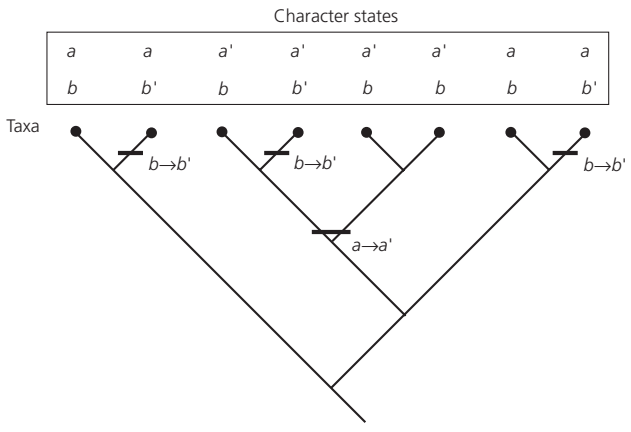

Fig. 4.1.1.5 Cladogram for eight hypothetical taxa, showing distribution of derived character states *a'* and *b'*, relative to primitive states *a* and *b*. Note congruence of homological similarities (shared *a'*), inherited from common ancestor, but incongruence of analogical (homoplasious) similarities (*b'*), on separate branches.

A clear example of the distinction between homological and analogical similarities is provided by solitary rugose corals, richthofeniacean brachiopods, and rudist bivalves. All three possessed conical to cylindrical shells of superficially similar form (Fig. 4.1.1.6), to the extent that at least one palaeontologist was tempted to infer phylogenetic links between them: 'As far as my opinion goes, I am convinced that *Richthofenia* is a member of a series, which, branching off somewhere from the rugose corals, has reached in *Richthofenia* a Brachiopod-like stage, and is going to terminate its career as a Pelecypod, as one of the *Rudista*…' (Waagen 1883, p. 18).

Other characters, however, clarify the respective taxonomic affinities of these three forms. Thus the pattern of radial septa of *Siphonophyllia* is diagnostic for rugose corals; the pseudopunctate calcite shell and symmetrical muscle scars of *Hercosestria* reveal it to be a strophomenide brachiopod; and the ligament, dentition, aragonitic inner shell, and adductor muscle scars of *Vaccinites* unmask it as a bivalve. The similarities between them are thus analogical (i.e. like the character state *b'* in Fig. 4.1.1.5). From a palaeoecological perspective, the convergence is instructive: the extended tubular shell form and tabulate filling of its lower part can be interpreted as a common adaptive response by sessile accretionary shell-growers for upward growth of the feeding system. Reasons for this may involve crowding and/or growth in habitats with net positive sediment accumulation, particularly in the cases of the coral and the rudist (of 'elevator' morphotype; Gili *et al.* 1995).

This stress on the value of analogical similarities does not necessarily mean that genealogical relationship (i.e. homological similarity) is uninformative concerning palaeoecology. The shared body plan of a given clade of organisms may constrain the adaptive scope of their life habits. An example is the virtual restriction of echinoderms to marine environments. However, such generalizations must be based on sound evidence. The example of echinoderm distribution seems secure, both because of the large number of living forms which all conform with the generalization, and because of the apparent absence in their body plan of any specialized system for

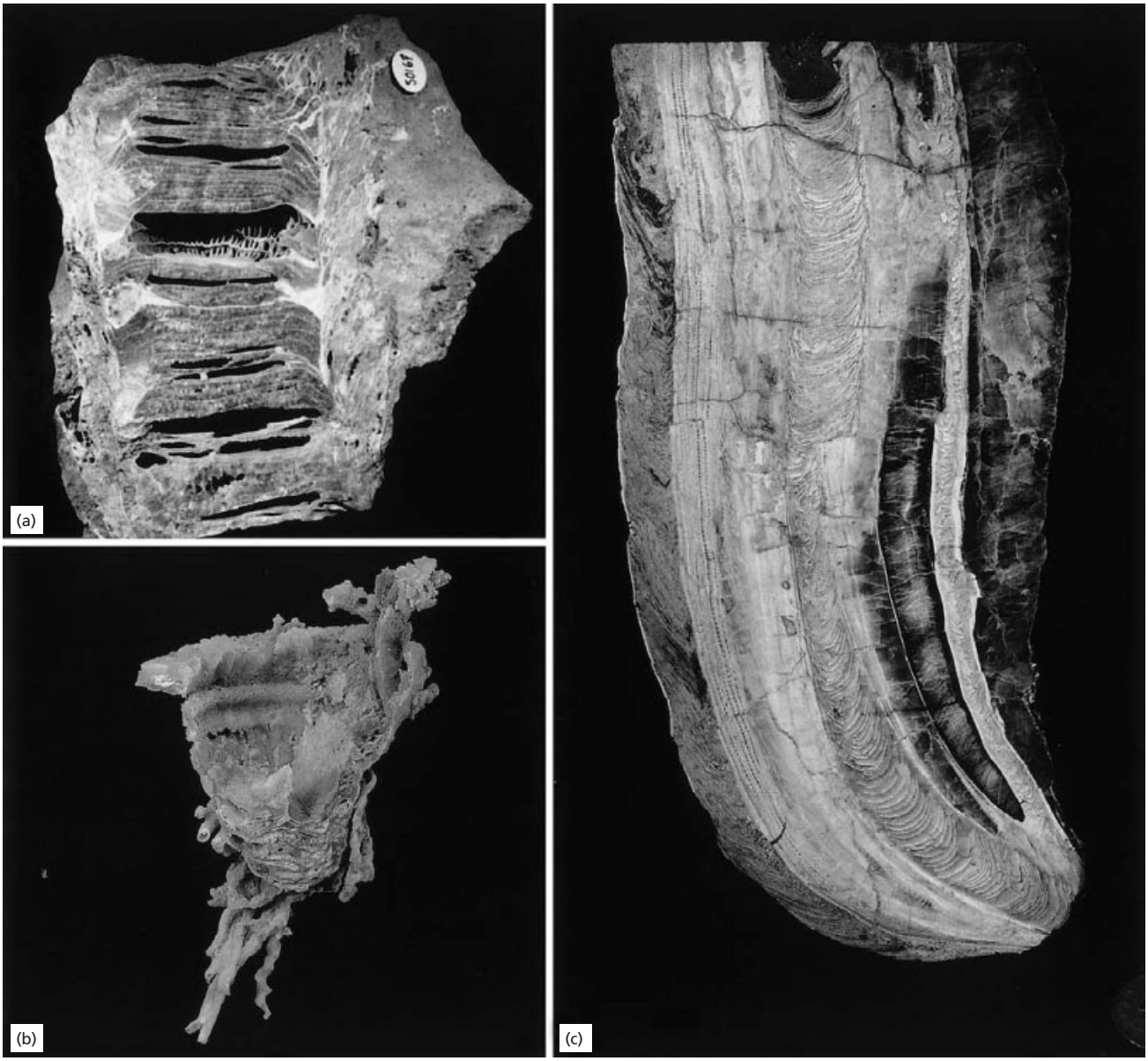

Fig. 4.1.1.6 (a) Carboniferous solitary rugose coral *Siphonophyllia*, ×0.8. (b) Permian richthofeniacean brachiopod *Hercosestria*, ×2.0. (c) Cretaceous rudist bivalve *Vaccinites*, ×0.6. (b, Courtesy of Sarah Long, Natural History Museum, London; a,c, from the collections of the Natural History Museum, London.)

countering osmotic stress. Any exceptional pioneer in fresh water would stand out as a markedly unusual kind of echinoderm.

On the other hand, a cautionary counter-example is provided by cycads. Living forms are frost-sensitive evergreen plants, restricted to low latitudes (Fig. 4.1.1.7a). So the presence of fossil cycad leaves (*Nilssonia*) in the Cretaceous of Alaska, in deposits originally laid down well within the Arctic Circle, appeared to pose a paradox (Spicer 1997): if Cretaceous polar temperatures had indeed remained warm enough throughout the year to allow such forms to survive, then the plants' respiration during the dark Arctic winter would have used up their food reserves, leading to starvation and death. Some researchers even toyed with the idea of major changes in the Earth's obliquity of rotation, to explain how such latitudes might have enjoyed some winter light. Resolution of the paradox came with the discovery of fossil stems (given the name *Nilssoniocladus*) bearing *Nilssonia* leaves (Fig. 4.1.1.7b). In complete contrast to the

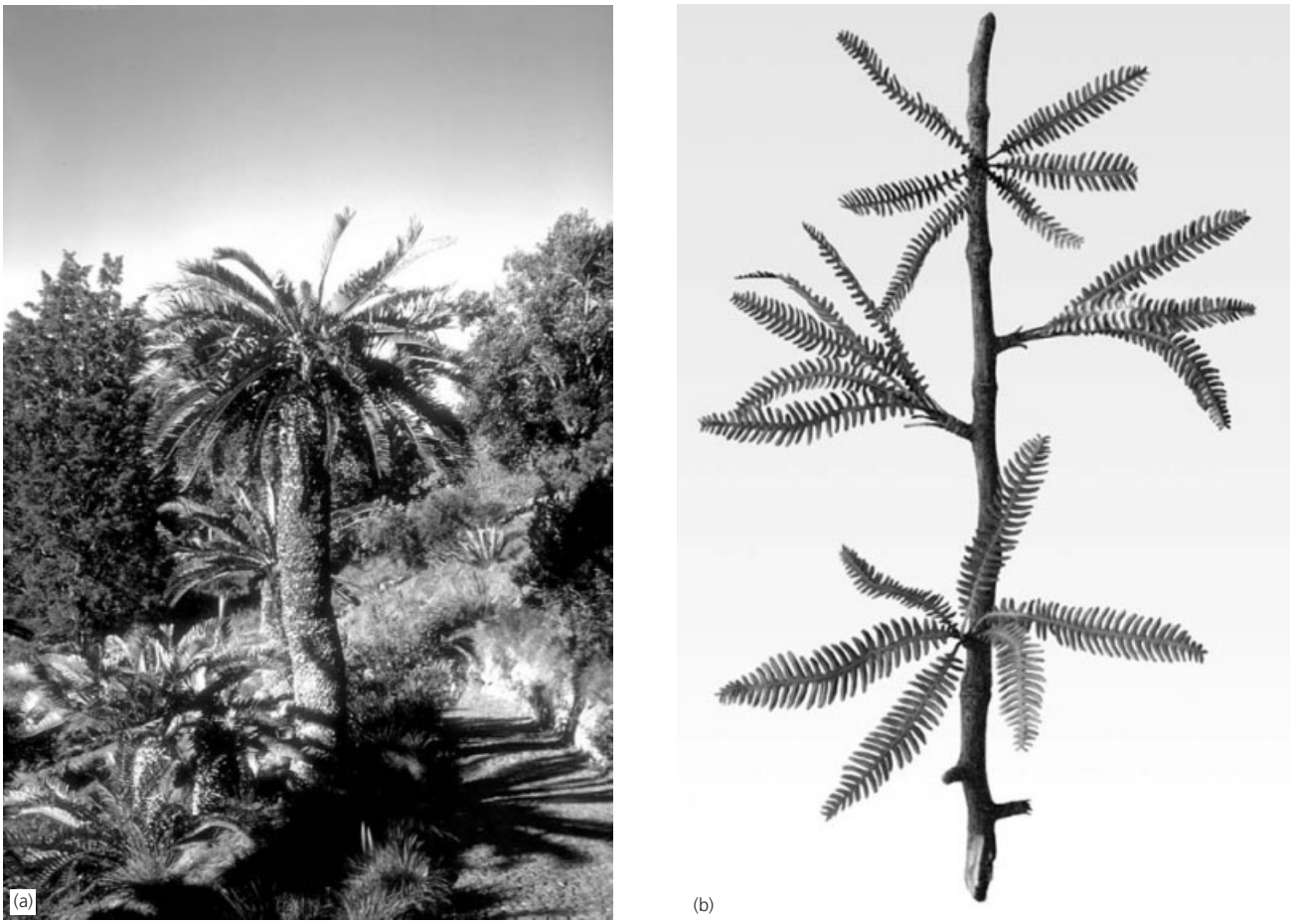

Fig. 4.1.1.7 Cycads. (a) Living *Encephalartos*, Cape Province, South Africa. (b) Reconstruction of stem of Cretaceous vine-like form, *Nilssoniocladus*. (Courtesy of John Watson, Open University.)

compact palm-like appearance of modern forms, this cycad was vine-like. Side shoots on the stem show numerous scars where whole leaves have been shed. So this cycad was evidently deciduous, unlike the living examples, coping with the long winter months of darkness by annually shedding its leaves. In this case, homology proved unreliable, and analogy with unrelated living taxa (indicating deciduousness) provided the better clue to the plants' way of life. A critical approach to inferences from homological similarity is therefore necessary.

Inference by analogy need not be limited to comparison with other organisms. A given feature might be interpreted by reference to a mechanical or even theoretical model (paradigm) of similar form, designed for a known function. Optimal 'design' should not always be expected in organisms, however, because of the constraints imposed both by their mode of construction and by conflicting functional requirements. But where it is detected, the plausibility of the functional hypothesis is greatly strengthened. A celebrated example is the analysis of the schizochroal eye in phacopinid trilobites (Clarkson and Levi-Setti 1975). The optical properties of the eye lenses were found to conform remarkably closely with idealized lens designs, demonstrating their capability, and hence their likely function, as image-forming devices.

Finally, it should be noted that the components of a given body plan today, i.e. the homologies found within a higher taxon, are themselves likely to have become fixed in a single ancestral population as an adaptive response to prevailing circumstances. Evolution thus involves the progressive accretion of adaptive modifications, a view enshrined in the conceptual framework of 'morphodynamics' (Seilacher 1991). According to this perspective, form evolves through the interplay of the functional and fabricational attributes of organisms with Darwinian selection exercised by their effective environment, forever building on the phylogenetic legacy of previous such interactions. As adaptive

modifications migrate up the genealogical hierarchy, so to speak, their original functions may fade as the context of interactions changes. So the more recent they are within a phylogeny, the more reliable they are likely to be as clues to palaeoecology.

Circumstantial evidence and testing of hypotheses

Science is characterized by the testing of hypotheses. Those discussed here concern events and relationships in the past. Experiments can only focus on the performance of similar living organisms (or models) for analogical comparison. Recreating the past in all its details, for experimental manipulation, is obviously out of the question.

The approach to hypothesis-testing most widely adopted in practice is to seek corroboration from other, independent lines of evidence: the more observations that yield the same conclusion, the more robust the explanatory power of an hypothesis. The principle involved was termed consilience (a 'jumping together' of inferences) by the English philosopher of science William Whewell (1794–1866). It is not quite the same as the currently fashionable Popperian criterion of failure to falsify an hypothesis (as employed in experimental physics, for example): it is often difficult to exclude mitigating explanations for apparently falsifying observations when dealing with the real complexities of nature, as opposed to a simple laboratory experiment.

A diversity of analytical approaches offer considerable scope for testing palaeoecological hypotheses in this way. For example, measurements of carbon and oxygen isotope ratios in the shells of fossil planktic foraminifers were used to test an hypothesis of depth stratification, which was based on analogy with the distribution of living morphotypes (Corfield and Cartlidge 1991). Today, keeled forms occupy relatively deeper waters than unkeeled forms. The test was based on the characteristic pattern of variation of the stable isotope ratios with depth. Thus, $^{18}O/^{16}O$ isotope ratios in shell carbonate tend to increase with depth (at least in the upper parts of the oceans), reflecting decreasing water temperature, while the $^{13}C/^{12}C$ isotope ratios of the shells generally decrease with depth as a consequence of preferential sequestering of ^{12}C in photosynthesized organic matter in surface waters. The results were equivocal, confirming the modern pattern for some time intervals (especially the Holocene and late Neogene), but not for others—perhaps signalling the dangers of overgeneralizing from today's pattern.

A commonly used test strategy is to confront inferences based upon morphology with those derived from sedimentological analysis. Assertions of pelagic, as opposed to benthic, life habits for various organisms have frequently been tested by reference to the relative degree of facies dependence of their fossils: indiscriminate distribution in different sediment types, especially where these include euxinic facies otherwise lacking a benthic biota, may be taken as vindicating such an hypothesis. Likewise, the evidence of body fossils may be compared with that from trace fossils. The gait of extinct tetrapods such as dinosaurs, for example, can be cross-checked from biomechanical analysis of their skeletons and from study of their footprints (see Section 4.1.11).

An interesting confrontation of experimental results and stratigraphic data was used to demonstrate the likelihood that the cemented habit in bivalves (e.g. in oysters) arose as a defensive adaptation against predators (Harper 1991). The experimental work compared the survivorship of byssate vs. cemented prey in the presence of known molluscivores (crabs and sea-stars). One species (the edible mussel, *Mytilus edulis*) was used for both prey types, to exclude the possibility of gastronomic bias by the predators—cementation being simulated with the aid of epoxy glue. The results (Fig. 4.1.1.8) showed that cementation conferred a significant advantage, at least with respect to these predators. Meanwhile, a review of the fossil record revealed a distinct clustering of first appearances of cemented bivalve clades in the Mesozoic, coinciding with the already well-documented expansion of durivorous predators associated with the 'Mesozoic marine revolution' (see Section 1.4.1). The consilience of these two quite separate lines of evidence renders the hypothesis that cementation arose in response to predation pressure more likely than the earlier, untested idea that it originated as an adaptation for resisting wave-surge.

Interpreting how fossil organisms lived

A procedure

The considerations outlined above allow the formulation of a general procedure for interpreting how organisms lived from their fossilized remains.

1 Detect homologies with other taxa, especially living forms, as far as possible, to establish a taxonomic identity for the fossil material.

2 Guided by the known body plan for the higher taxon to which the material has been assigned, reconstruct the basic anatomy of the original organism. The specific form (e.g. disposition of muscle scars) of the preserved homologous components can help to fine-tune the reconstruction and/or highlight any special modifications of the body plan.

3 Consider any well-established palaeoecological gen-

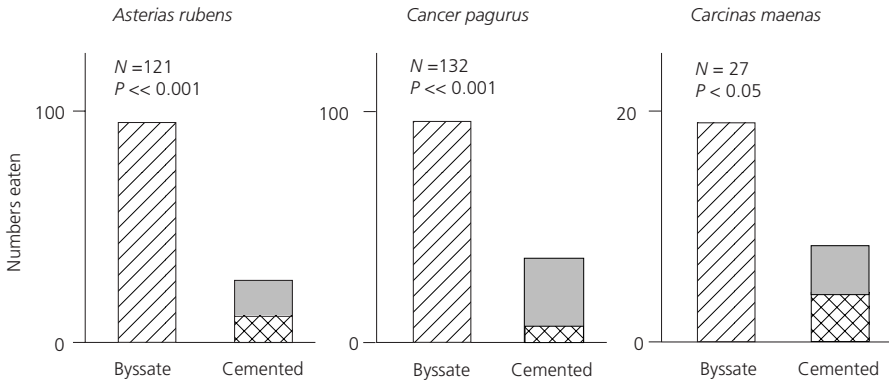

Fig. 4.1.1.8 Histograms showing numbers of byssate vs. 'cemented' (epoxy-attached) mussels (*Mytilus edulis*) successfully eaten by selected predators, when presented with equal numbers of the two prey types. The predators were the common starfish (*Asterias rubens*) and two widespread species of crabs (*Cancer pagurus* and *Carcinas maenas*). The total of 'cemented' prey eaten in each histogram conflates those eaten in place (lower part of bar) and those pulled free and then eaten (upper, shaded part of bar). (Based on Harper 1991.)

eralizations associated with the higher taxon in question, checking that no special modifications of the body plan, or other evidence, contradict them.

4 Within the constraints established above, hypothesize the possible functional capabilities of features by analogy with: (a) other living organisms of similar form; and/or (b) mechanical or theoretical models designed for specific functions. Such hypotheses can be checked by critical comparison of the features in question with the functional specifications of the models.

5 Other lines of evidence can now be pursued by way of testing. The nature of the original organism's habitat and environment (including biotic interactions) can be variously inferred from associated sedimentological, taphonomic, geochemical, trace fossil, and other palaeoecological evidence.

An example

The ammonites provide an illustration of the application of the successive stages of this procedure.

1 The chambered shell with its siphuncle readily places ammonites among cephalopod molluscs.

2 The living *Nautilus*, though differing in details, shares retention of the external shell (a primitive character state) with the ammonites. It can therefore serve as a model for reconstructing the basic anatomy of the latter, by homological inference; muscle scars, as well as other occasionally preserved features in the fossils, such as radulae and jaws, provide more specific clues (Kennedy and Cobban 1976).

3 There is no reason to doubt (from the form of the siphuncle) that the chambers became gas-filled, as in *Nautilus*, to provide buoyancy. Yet the shape of the body chamber indicates a relatively narrow but elongate body and mantle cavity, leaving open to question the extent of the ammonites' ability to swim by jet propulsion, in the manner of *Nautilus*. External shell form also shows much variation, with implications for swimming capabilities.

4 Limits on the possible swimming capabilities of differently shaped ammonites can be assessed by analogy with a representative set of geometrically precise models (Chamberlain 1980). Contours of drag coefficient, based on experimental measurements from the models, can be plotted on the field of planispiral geometries defined by axes for whorl expansion rate (W) and whorl distance from the coiling axis (D) (Fig. 4.1.1.9). The clumping of weakly ornamented, planispiral ammonites around one of the two areas of minimum drag coefficient on the plot indicates that, for these forms at least, shell shape was more or less optimal for swimming. So active swimming was probably an important part of their mode of life (i.e. a functional selective constraint on form). However, the absolute drag values show that these ammonites were still considerably less efficient swimmers than torpedo-shaped hunters, such as barracuda, shark, and squid. Active pursuit of swimming prey was unlikely; passive capture was more probable. Dodging out of the way of lunging predators was a more likely selective pressure on swimming ability.

5 That most such ammonites were indeed pelagic is confirmed by their distribution in a variety of open marine facies. The relative facies dependence of other types, by contrast (e.g. most heteromorphs and strongly ornamented forms), implies more bottom-dwelling habits. Occasionally preserved gut contents imply feeding on small prey (even cannibalism of juveniles) to scavenging in most forms (Kennedy and Cobban 1976).

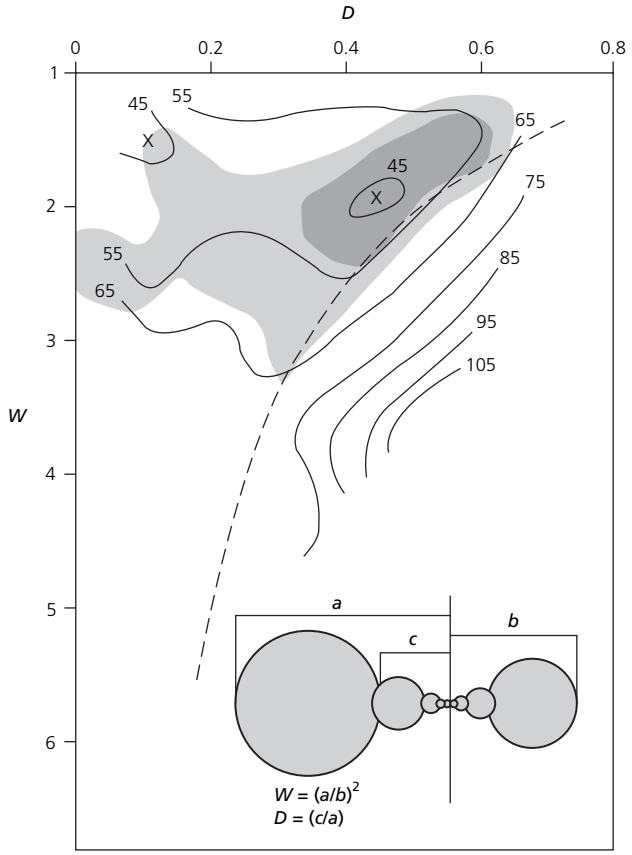

Fig. 4.1.1.9 Contours of drag coefficient (×100) plotted on the field of possible planispiral coiling geometries defined by whorl expansion rate (*W*) and relative whorl distance from the coiling axis (*D*) (see inset diagrammatic section across coiled shell for definitions of *W* and *D*). The two points marked X indicate shell forms with minimum drag. The dashed line separates shells with whorl overlap (left and above) from those with loose, non-overlapping whorls (below). The shaded area shows the distribution of 90% of weakly ornamented planispiral ammonites sampled, the majority falling within the darker area. (Modified from Chamberlain 1980, with permission.)

Hence the picture that emerges is of the smoother, discoidal ammonites, at least, floating and swimming to a limited extent in open water, and probably relying on passive capture of passing prey (?mainly plankton), while many other forms adopted more nektobenthic habits, feeding on a range of bottom-dwelling organisms or detritus.

References

Briggs, D.E.G., Clarkson, E.N.K. and Aldridge, R.J. (1983) The conodont animal. *Lethaia* **16**, 1–14.

Chamberlain, J.A. (1980) Hydromechanical design of fossil cephalopods. In: M.R. House and J.R. Senior, eds. *The Ammonoidea*, pp. 289–336. Systematics Association, Special Volume 18. Academic Press, London.

Clarkson, E.N.K. and Levi-Setti, R. (1975) Trilobite eyes and the optics of Descartes and Huygens. *Nature* **254**, 663–667.

Conway Morris, S. and Peel, J.S. (1990) Articulated halkieriids from the Lower Cambrian of Greenland. *Nature* **345**, 802–805.

Corfield, R.M. and Cartlidge, J.E. (1991) Isotopic evidence for the depth stratification of fossil and Recent Globigerinina. *Historical Biology* **5**, 37–63.

Eldredge, N. (1985) *Unfinished synthesis—biological hierarchies and modern evolutionary thought*. Oxford University Press, New York and Oxford.

Gili, E., Masse, J.-P. and Skelton, P.W. (1995) Rudists as gregarious sediment-dwellers, not reef-builders, on Cretaceous carbonate platforms. *Palaeogeography, Palaeoclimatology and Palaeoecology* **118**, 245–267.

Harper, E.M. (1991) The role of predation in the evolution of cementation in bivalves. *Palaeontology* **34**, 455–460.

Kennedy, W.J. and Cobban, W.A. (1976) Aspects of ammonite biology, biogeography, and biostratigraphy. *Special Papers in Palaeontology* **17**.

Knoll, A.H. and Calder, S. (1983) Microbiotas of the late Precambrian Ryssö Formation, Nordaustlandet, Svalbard. *Palaeontology* **26**, 467–496.

Pojeta, J. Jr (1980) Molluscan phylogeny. *Tulane Studies in Geology and Paleontology* **16**, 55–80.

Rollins, H.B. and Batten, R.L. (1968) A sinus-bearing monoplacophoran and its role in the classification of primitive molluscs. *Palaeontology* **11**, 132–140.

Runnegar, B., Pojeta, J. Jr, Taylor, M.E. and Collins, D. (1979) New species of the Cambrian and Ordovician chitons *Matthevia* and *Chelodes* from Wisconsin and Queensland: evidence for the early history of polyplacophoran mollusks. *Journal of Paleontology* **53**, 1374–1394.

Schidlowski, M. (1988) A 3,800-million-year isotopic record of life from carbon in sedimentary rocks. *Nature* **333**, 313–318.

Seilacher, A. (1991) Self-organizing mechanisms in morphogenesis and evolution. In: N. Schmidt-Kittler and K. Vogel, eds. *Constructional morphology and evolution*, pp. 251–271. Springer-Verlag, Berlin and Heidelberg.

Spicer, R.A. (1997) Polar climate. In: P.W. Skelton, R.A. Spicer and A. Ries. *Evolving life and the Earth*, pp. 129–139. Open University, Milton Keynes.

Waagen, W. (1883) On the genus *Richthofenia*, Kays. (*Anomia Lawrenciana*, Koninck). *Records of the Geological Survey of India* **16**, 12–19.

Yochelson, E.L. (1966) Mattheva, a proposed new class of mollusks. *United States Geological Survey, Professional Paper* **523B**, B1–B11.

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4.1.2 Stromatolites

M.R. WALTER

Introduction

Benthic microbial mats are common today, though sporadically distributed, but prior to the rise to dominance of metazoans some 600 myr ago, they were ubiquitous in the subaqueous photic realm, abundant in deeper waters, and probably widespread on land. They leave a record as kerogen, biomarker hydrocarbons, carbon and sulphur isotope signatures, and stromatolites. Stromatolites are biosedimentary structures generated by benthic microbial mats and biofilms, as a result of trapping of particulate sediment or the templating of mineral precipitation. In seeking the light, and perhaps for other reasons, the microbes built sedimentary structures with vertical relief, at every scale from the microscopic to the monumental. During the Proterozoic, bizarre 'forests' of giant conical stromatolites, like rocket nose cones placed edge to edge, were a common feature of the sea floor. Branching forms as diverse as modern corals were abundant (Walter 1976, 1994). They created reefs as big as any later built by corals and algae, and they participated in the construction of continental shelves and ramps with facies architectures like those of the Phanerozoic (Grotzinger 1989).

In the Proterozoic, almost all little-metamorphosed limestones, dolomites, and magnesites contain stromatolites, and they also occur in phosphorites, iron-formations, cherts, and (rarely) in sandstones. For more than 3 billion years microbial mats sculpted the sea floor and exploited the chemical potential of the sediment–water interface. They did the same in lakes, and can be expected to have colonized the land.

Following the original definition, the term 'stromatolite' is usually restricted to laminated structures. Microbial deposits which lack lamination and have a 'clotted' fabric are called 'thrombolites' and the term 'microbialite' is often used to refer to all microbial deposits. Here stromatolite is used as a synonym for microbialite (but see Grotzinger and Knoll 1999). Terms such as 'cryptalgal laminite' and 'algal stromatolite' are now misleading and inappropriate for several reasons, but especially because biologists 30 years ago recognized that the 'blue–green algae' which construct most stromatolites are in fact bacteria (cyanobacteria) and not algae.

Evolution of stromatolites

The inhabitants of stromatolite-building microbial mats include representatives of all three currently recognized superkingdoms of life (Bacteria, Archaea, and Eukarya). Most ancient stromatolites seem to have been constructed by cyanobacteria, although that is demonstrable in only a small number of examples. Certainly, most presently known modern stromatolites are cyanobacterial, though microalgae such as diatoms are prominent members of the mat community in subaqueous examples (Fig. 4.1.2.1b). Even in 'extreme' environments, such as hypersaline tidal flats, the mat communities are complex. They include the primary producers that generate the architecture of the mats, photosynthetic bacteria living a millimetre or so below the mat surface which use the light that filters through the surface cyanobacteria, and aerobic and anaerobic heterotrophic bacteria, such as sulphate-reducers, which break down the mats. Living within this fabric is a meiofauna which includes nematodes and annelids. The mats are grazed by gastropods, fish, and other metazoans, and provide a substrate for the growth of macroscopic algae. Hollows within lithified stromatolites are frequently populated by sponges, tube-building annelids, foraminiferans, and shrimps (Table 4.1.2.1).

The Palaeoarchaean stromatolites (see Section 1.1.3) of hypersaline lagoons were probably built by photoautotrophs, but they may have been anaerobic photosynthetic bacteria rather than aerobic oxygenic cyanobacteria. By the Neoarchaean the evidence strongly suggests that cyanobacteria were the constructors of stromatolites. There is a very high diversity of stromatolites in Palaeoproterozoic successions, and some were demonstrably built by cyanobacteria. Temporal restriction of numerous stromatolite forms during the Proterozoic seems to reflect both microbial evolution and an evolving environment. It is not clear when eukaryotic microalgae first became part of the stromatolite-building mat communities: there is good evidence for them in the latest Neoproterozoic, and equivocal evidence back as far as the Palaeoproterozoic. Enrichment of cyanobacterial mats by microalgae may explain the high taxonomic diversity of stromatolites in Mesoproterozoic and early Neoproterozoic successions (the taxonomy of stromatolites is a controversial matter, given that they are biosedimentary structures formed by diverse communities of microbes; none the less, biostratigraphers treat them in much the same way as trace fossils).

At some ill-defined time, animals invaded the mat ecosystem. Cambrian mats, like their extant analogues, were bored, burrowed, and grazed by metazoans. At about the beginning of the Neoproterozoic something happened to lower the diversity of stromatolites in quiet subtidal environments, and in the mid to late Neoproterozoic the diversity of all stromatolites declined drastically. As yet there is no direct evidence of the cause or causes of these events, but the simplest explanation is that the disruption of mats by metazoans started in the

Fig. 4.1.2.1 Stromatolites in Hamelin Pool, Shark Bay, Western Australia. (a) Elongate forms in the intertidal zone; the elongation is perpendicular to the shoreline; these are constructed by the coccoid cyanobacterium *Entophysalis* sp. (b) Subtidal forms in 2–3 m of water; diverse communities of cyanobacteria and microalgae, including diatoms, occur in these, and abundant macroscopic algae are attached to them. (a, Photograph by P. Hoffman.)

Table 4.1.2.1 Census of the protists and animals found in, on, and amongst the stromatolites of Hamelin Pool, Shark Bay, Western Australia. (From Walter 1994.) The list is certainly not complete, but it serves to illustrate the species richness of this stromatolite ecosystem, despite the hypersalinity of the waters. Comparable ecosystems must have evolved during the Neoproterozoic, and are documented in the early Palaeozoic. They are also found in lakes (Freytet and Verrecchia 1998).

	Species	Size (mm)	Food source
Mammals (dugong)	1	≈ 3000	Sea grass
Fish	15	8–1500	Fish
			Crustaceans
			Detritus in sand
			Plankton
Reptiles (sea snake)	1	≈ 1000	Fish
Bivalves	5	2–15	Suspended organic matter
Gastropods	5	1–2	Cyanobacteria?
Crustaceans	5	0.5–35	Plankton
			Organic detritus
Annelids	2	0.5–5	Small animals
			Suspended organic matter
Coelenterates (medusa)	1	100–300	Suspended organic matter
Nematodes	30	< 1	Bacteria
			Algae
			Small animals
Foraminifera	10	< 1	Bacteria
			Organic detritus
Sponges	3	5–15	Suspended organic matter

subtidal realm during the early Neoproterozoic and spread later to the intertidal environment. Decreased bicarbonate concentrations in the oceans, and displacement of mats by newly evolved macroalgae, could also have been factors. Stromatolites continued to form throughout the Phanerozoic, and while still abundant in such 'extreme' environments as hypersaline tidal flats and thermal springs, in submarine environments they were far less prominent than before. Exceptions, such as the Devonian reefs of Western Australia and the platform deposits of the Triassic of Germany, may represent a temporary return to prominence after major metazoan extinction events. There appears to have been less of a decline in lacustrine environments. Stromatolites were prominent in lakes during the Proterozoic (e.g. Hill *et al.*, in press) and the Phanerozoic (e.g. the Eocene Green River Formation, Wyoming), and remain so.

Stromatolite recognition

Distinguishing stromatolites from abiological but comparable structures is a vexed issue (see Section 1.1.3). It has long been recognized that abiotic mineral precipitates can mimic features of stromatolites. The only presently known compelling criterion (but see Hofmann *et al.* 1999) for demonstrating that a structure is a stromatolite is the presence of a fossil microbiota with cell orientations that indicate a role in constructing the sedimentary architecture. Such examples are known, but are relatively rare. A number of criteria provide a convincing argument that most structures identified as stromatolites by experts in the field are indeed biogenic: (1) there are examples with microfossils arranged in patterns indicating that they were responsible for the construction of the laminae of the stromatolites; (2) the distribution of stromatolite-dominated carbonate sedimentary facies in the Proterozoic matches that of algal- and coral-dominated facies in the Phanerozoic, reflecting comparable biological influences; (3) there are numerous modern stromatolites where biological influences in morphogenesis can be directly observed; and (4) in the modern world it is difficult to find any stromatolite-like objects which are demonstrably abiotic (e.g. what used to seem like an excellent example of the latter, the high-temperature geyserites of hot springs, has recently been demonstrated to be inhabited by microbial biofilms that apparently play a critical role in the morphogenesis of the geyserite).

The role of biofilms in mineral precipitation and sediment morphogenesis is as yet little known, but given the pervasive (ubiquitous?) presence of life in environments cooler than 150°C or so, it is reasonable to expect a significant role for these organic structures. Organic molecules and structures play an important role in providing templates for catalysing and ordering mineral deposition (Banfield and Nealson 1997). It is likely that all mineral structures that formed at less than about 150°C in the presence of water were influenced by microbes. The question is not whether they are biogenic, but the extent of the biogenicity.

None the less, many of the features of stromatolites that are often tacitly assumed to be biogenic are just as likely to be abiotic (Grotzinger and Knoll 1999). In the one example studied, over three orders of magnitude in size, the stromatolite laminae as seen in the field and on cut slabs obey the same power law. From this the fractal dimension of the stromatolites is obtained, and used to deduce the processes of stromatolite growth. The morphogenesis of these stromatolites can be accounted for by four abiotic processes: (1) fallout of suspended sediment, (2) downslope movement of that sediment (or the mathematically equivalent surface-tension effects in chemical precipitation), (3) surface-normal precipitation, and (4) random effects. Theoretically, abiotic processes could have generated these stromatolites, and in the absence of included microfossils biogenicity may be unprovable. However, the origin of the microscopic surface roughness postulated to be responsible for generating the macroscopic stromatolitic structure was not explained. The roughness—microscopic pinnacles perpendicular to sedimentary lamination—can be compared with calcified cyanobacteria (Freytet and Verrecchia 1998). So, if the analysis is valid, it could prove biogenicity, rather than the opposite.

Patterns in the distribution of stromatolites through time

1 Palaeoarchaean and Mesoarchaean stromatolites were rare and not diverse.

2 In the Neoarchaean, about 2.7–2.8 Ga, stromatolites were more abundant and much more diverse. This may have resulted from the formation, for the first time, of extensive continental shelves.

3 Amongst the columnar forms that rose to prominence in the Neoarchaean and especially in the Palaeoproterozoic was an abundance of ministromatolites with a radial fibrous fabric, characteristic of peritidal environments; these declined markedly after the Mesoproterozoic. The biogenicity of these is contentious.

4 In the Palaeoproterozoic and Mesoproterozoic, there was an abundance of stromatolites with conical laminae (called *Conophyton* and various other names by biostratigraphers), characteristic of quiet subtidal environments. They declined markedly thereafter (Grotzinger and Knoll 1999 and references therein).

5 There was a decline in abundance and diversity of all stromatolites about 600–700 Ma (Grotzinger and Knoll 1999 and references therein).

6 Thrombolites (unlaminated stromatolites) were rare

before the Phanerozoic and became abundant during the Early Cambrian (Kennard and James 1986).
7 Stromatolites are rare after the Early Ordovician, except in marine supratidal and lacustrine settings.
8 The preservation of microscopic microbial fabrics showing traces of cell morphology in carbonate stromatolites is rare in the Archaean and Proterozoic but common in the Phanerozoic; this seems to be yet another example of the appearance of calcification near the base of the Cambrian.

Within this framework many finer patterns have been recognized, and are used in biostratigraphy and palaeoenvironmental interpretations. Stromatolite biostratigraphy has been a controversial field, but it has been used now for more than 50 years, mostly in the Proterozoic, and the evidence that it works is compelling.

References

Banfield, J.F. and Nealson, K.H. (1997) *Geomicrobiology: interactions between microbes and minerals*. Reviews in Mineralogy, no. 35. Mineralogical Society of America, Washington DC.

Freytet, P. and Verrecchia, E.P. (1998) Freshwater organisms that build stromatolites: a synopsis of biocrystallization by prokaryotic and eukaryotic algae. *Sedimentology* **45**, 535–563.

Grotzinger, J.P. (1989) Facies and evolution of the Precambrian carbonate depositional systems: emergence of the modern platform archetype. *Special Publication of the Society of Economic Paleontologists and Mineralogists* **44**, 79–106.

Grotzinger, J.P. and Knoll, A.H. (1999) Stromatolites in Precambrian carbonates: evolutionary mileposts or environmental dipsticks? *Annual Review of Earth and Planetary Sciences* **27**, 313–358.

Hill, A.C., Al Arouri, K., Gorjan, P. and Walter, M.R. (in press) Sedimentology, paleobiology and paleoenvironments of a cratonic carbonate platform: the Neoproterozoic Bitter Springs Formation, Amadeus Basin, central Australia. *Special Publication of the Society of Economic Paleontologists and Mineralogists*.

Hofmann, H.J., Grey, K., Hickman, A.H. and Thorpe, R.I. (1999) Origin of 3.45 Ga coniform stromatolites in Warrawoona Group, Western Australia. *Bulletin of the Geological Society of America* **111**, 1256–1262.

Kennard, J.M. and James, N.P. (1986) Thrombolites and stromatolites: two distinct types of microbial structures. *Palaios* **1**, 492–503.

Walter, M.R., ed. (1976) *Stromatolites*. Developments in Sedimentology, no. 20. Elsevier, Amsterdam.

Walter, M.R. (1994) Stromatolites: the main source of information on the evolution of the early benthos. In: S. Bengtson, ed. *Early life on Earth*, pp. 270–286. Nobel Symposium no. 84. Columbia University Press, New York.

4.1.3 Plant Growth Forms and Biomechanics

T. SPECK and N.P. ROWE

Introduction

Palaeobotanical research aims to reconstruct fossil plants, their form and size, life histories, and ecosystems. In order to begin to understand the specific ecological niche occupied by a fossil plant species, its many structural, physiological, and biochemical properties must be considered, in addition to biotic and abiotic environmental factors. It is difficult to analyse fossil plants because of inadequate preservation and the often disarticulated nature of the material. These problems make it particularly difficult to infer growth forms and the attitude of fossil plants in their original habitat. Size, shape, and posture are important aspects of a plant's growth form and can be used to infer a range of ecological preferences of long-extinct plants. Based on experiments with living plants, growth forms and maximum heights of fossil plants can be quantitatively investigated by calculating the biomechanical properties of stem segments from different ontogenetic stages (Speck 1994; Speck and Rowe 1999a).

Methods

In order to assess the bending mechanical properties of stems, three fundamental parameters and their variation during ontogeny must be considered: (1) the flexural stiffness (EI) quantifies the ability of a stem to resist bending forces, and can be determined on the basis of bending tests on living plants; (2) structural Young's modulus (E) describes the stiffness of a stem in bending (the prefix 'structural' is used to emphasize that plant stems are inhomogeneous composite materials); and (3) the axial second moment of area (I) is a geometrical parameter that quantifies the cross-sectional size and shape of stems and tissues in relation to the direction of bending. In plants with secondary growth I can be used to approximate the ontogenetic sequence of stem development (Speck and Rowe 1999b).

Three main growth forms can be distinguished in living woody plants by quantitative analyses of biomechanical properties and structural changes during ontogeny (Speck and Rowe 1999b): (1) 'self-supporting' shrubs and trees show a significant increase in structural Young's modulus during ontogeny, caused by an increase in the amount of strengthening tissues (wood); (2) 'semi-self-supporting' (leaning) plants are character-

ized by a structural Young's modulus and stem structure that do not change significantly during ontogeny; and (3) 'non-self-supporting' lianas show a significant drop of structural Young's modulus during ontogeny, caused by a drastic reduction in the amount of strengthening tissues. Detailed analysis of the variation in mechanical properties and stem structure of a wider range of plants shows that this ontogenetic approach can reveal patterns of biomechanical behaviour characterizing a diversity of growth forms (Speck and Rowe 1999a,b).

The method can be extended to fossil material: the relevant parameters are calculated from the composition and arrangement of fossilized stem tissues (Fig. 4.1.3.1) (Speck 1994; Speck and Rowe 1999a). A range of ontogenetic stages (diameters) of the fossil plant stem are required; anatomy must be well enough preserved to allow the geometrical arrangement of the tissues and the structural features of cells comprising each stem tissue to be analysed quantitatively. By using experimentally measured data (Young's moduli) from similar extant tissues, the mechanical properties of different ontogenetic stages of the fossil stem can be calculated. Finally the growth form of the fossil plant can be inferred by comparing the patterns of variation in mechanical properties during ontogeny with those observed among tested living plants with known growth forms.

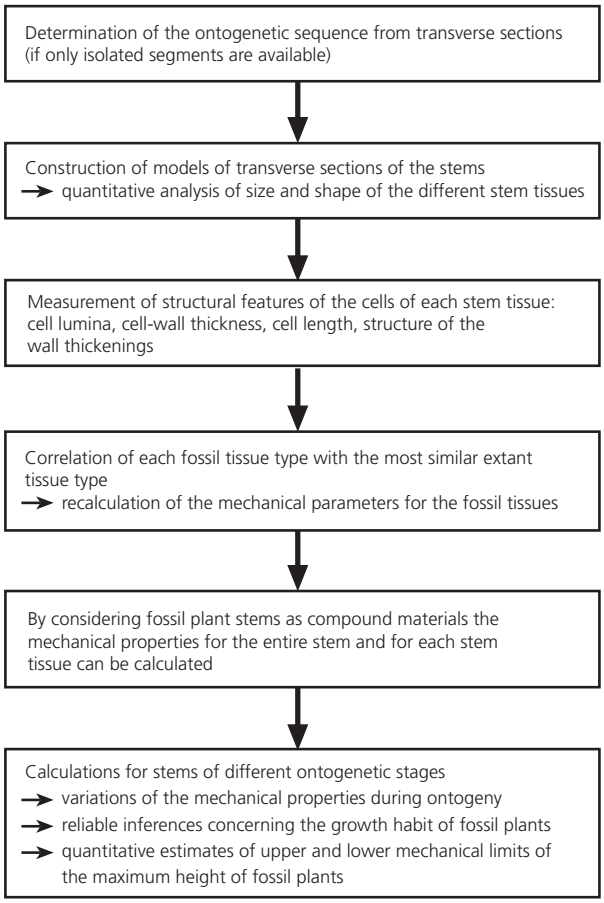
Determination of the ontogenetic sequence from transverse sections (if only isolated segments are available)
Construction of models of transverse sections of the stems
→ quantitative analysis of size and shape of the different stem tissues
Measurement of structural features of the cells of each stem tissue: cell lumina, cell-wall thickness, cell length, structure of the wall thickenings
Correlation of each fossil tissue type with the most similar extant tissue type
→ recalculation of the mechanical parameters for the fossil tissues
By considering fossil plant stems as compound materials the mechanical properties for the entire stem and for each stem tissue can be calculated
Calculations for stems of different ontogenetic stages
→ variations of the mechanical properties during ontogeny
→ reliable inferences concerning the growth habit of fossil plants
→ quantitative estimates of upper and lower mechanical limits of the maximum height of fossil plants

Fig. 4.1.3.1 Flow chart of the methodology used for analysing mechanical properties, functional anatomy, growth habit, and maximum height of fossil plants.

Results

The growth form of a variety of woody Palaeozoic species with secondary growth has been analysed, including *Diaphorodendron vasculare, Pitus dayi, Lyginopteris oldhamia,* and *Calamopitys* sp. (Speck 1994; Speck and Rowe 1994; Rowe and Speck 1998). In the first three plants the analysis was based on disconnected permineralized fragments from which a hypothesized ontogenetic sequence was constructed. With this type of data (termed 'general data' by Rowe and Speck 1998) it is impossible to distinguish between young growth phases of a species (i.e. seedlings or saplings) and young distal or regenerative shoots of a mature plant. However, this does not affect the validity of the analysis, as studies from a range of extant plants have shown (Speck and Rowe 1999b). *Diaphorodendron vasculare*, a Carboniferous rhizomorphic lycopsid, has been used to test the method, based on a reliable interpretation of its probable growth form and height. The calculated mechanical data are consistent with experimental data from extant self-supporting trees in which the structural Young's modulus increases significantly during ontogeny. In *D. vasculare* structural Young's modulus increases by a factor of about 3.5 (Figs 4.1.3.2a and 4.1.3.3a).

The biomechanical approach also allows maximum height to be calculated (Speck 1994). The calculated maximum height of *D. vasculare* of 12–20 m (Speck 1994) is consistent with that of about 15 m inferred from fossil material. *Pitus dayi* comprises exceptionally well-preserved young branch segments of a Lower Carboniferous seed plant. Calculations showed unequivocally that it was self-supporting (Figs 4.1.3.2b and 4.1.3.3b), suggesting that the isolated segments belong to a large-bodied arborescent plant. In *P. dayi*, some of the tissues could not be matched with living tissue types and known Young's moduli. To overcome this problem models were constructed with varying Young's modulus values representing different tissue types characteristic of the cortex/periderm. Despite the range of models tested, all the results clearly showed that the plant was self-supporting (Speck and Rowe 1994). Furthermore, large decorticated stumps and branches common in the Lower Carboniferous of Scotland appear to represent the stems and basal branches of *P. dayi*, allowing estimates to

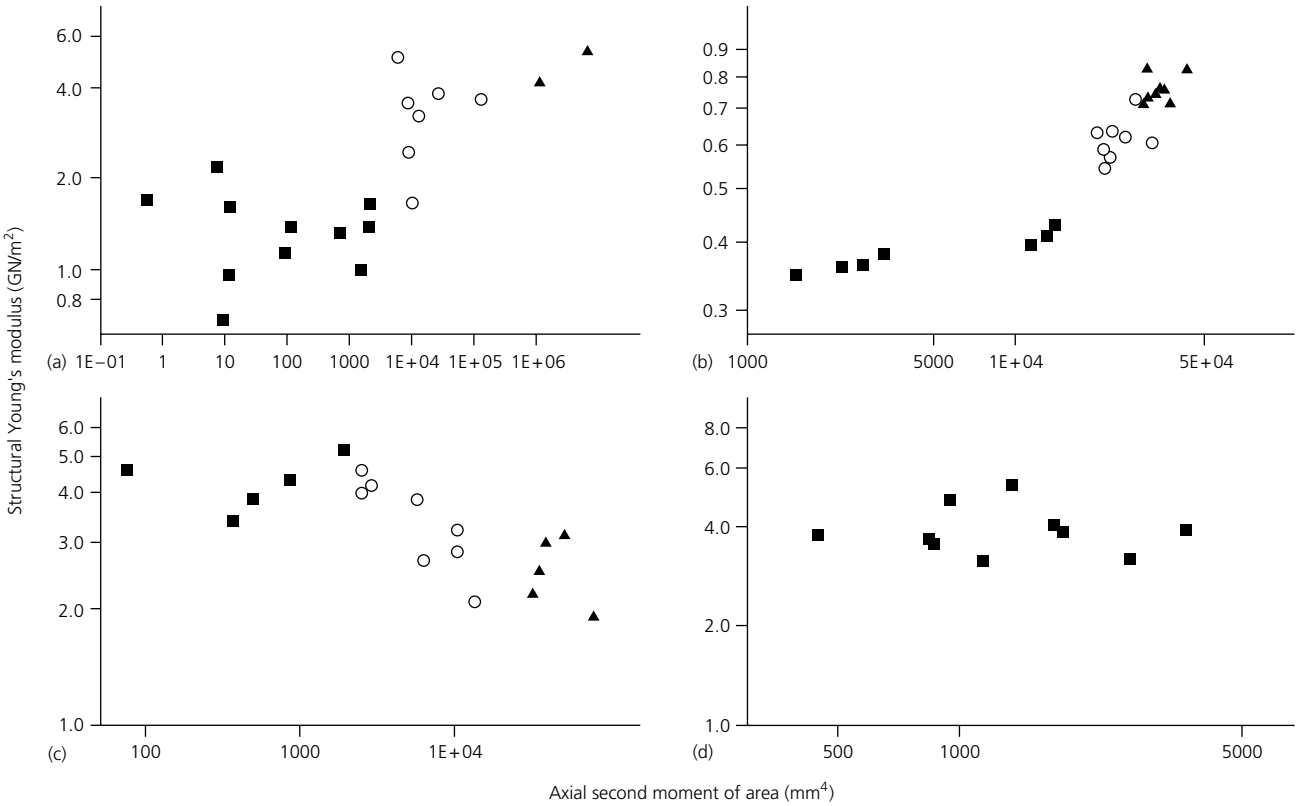
Structural Young's modulus (GN/m²)
(a) 1E−01 1 10 100 1000 1E+04 1E+05 1E+06
(b) 1000 5000 1E+04 5E+04
(c) 100 1000 1E+04
(d) 500 1000 5000
Axial second moment of area (mm⁴)

Fig. 4.1.3.2 Structural Young's modulus (*E*) calculated for selected fossil plants plotted against the axial second moment of area (*I*) (double logarithmic plots). In plants with secondary growth, the axial second moment of area can be correlated with the ontogenetic stage of the stems. (a) *Diaphorodendron vasculare*. (b) *Pitus dayi*. (c) *Lyginopteris oldhamia*. (d) *Calamopitys* sp. Symbols characterize different ontogenetic stages: ■, young ontogenetic stage; ○, middle-aged; ▲, old. The self-supporting growth form is characterized by a distinct increase of structural Young's modulus with ontogenetic stage, a data pattern found for *D. vasculare* and *P. dayi*. The semi-self-supporting growth form is characterized by a (nearly) constant structural Young's modulus during ontogeny, as found in *Calamopitys* sp. The data for *L. oldhamia* show only a slight decrease of structural Young's modulus during ontogeny; this pattern is more compatible with extant semi-self-supporting plants than angiospermous lianas, which show dramatic decreases in structural Young's modulus of up to 95%. (a,c, From Speck 1994, with permission from Elsevier Science; b, from Speck and Rowe 1994; d, from Speck and Rowe 1999b.)

be made of variations in the mechanical properties of the entire '*Pitus*-plant' (Rowe and Speck 1998).

The growth forms of at least two other Carboniferous pteridosperms have been controversial (*Lyginopteris oldhamia*) or could be inferred only from stem size and anatomy (*Calamopitys* sp.). *Lyginopteris oldhamia* shows a slight decrease in structural Young's modulus during ontogeny (Fig. 4.1.3.2c), a pattern that suggests that this plant was not self-supporting (Speck 1994). The structural Young's moduli calculated for *L. oldhamia* are relatively high compared with those of extant lianas, and decrease only to about 60% of their initial value, suggesting that *L. oldhamia* was a semi-self-supporting plant that may have become lianescent in old ontogenetic stages (Fig. 4.1.3.3c) (Speck and Rowe 1999b). The stem of *Calamopitys* is consistent with a semi-self-supporting growth form, as the structural Young's modulus remains nearly constant over the entire ontogenetic range tested (Figs 4.1.3.2d and 4.1.3.3d) (Rowe and Speck 1998). Data for the stem of *Calamopitys* are consistent with that of a semi-self-supporting stem, although all the points are derived from a single slender axis. The trend towards the base of the segment is not consistent with that of a self-supporting branch and appears to result from a constraint on the size of the primary body during ontogeny. The specimen tested was a permineralized plant stem, nearly 75 cm long, which provided an opportunity to study sections at known intervals along its length. Such 'positional data' supply information on the finer details of adaptive growth, such as structural and mechanical responses of the plant to the local environment. Positional data are particularly important for analysing the

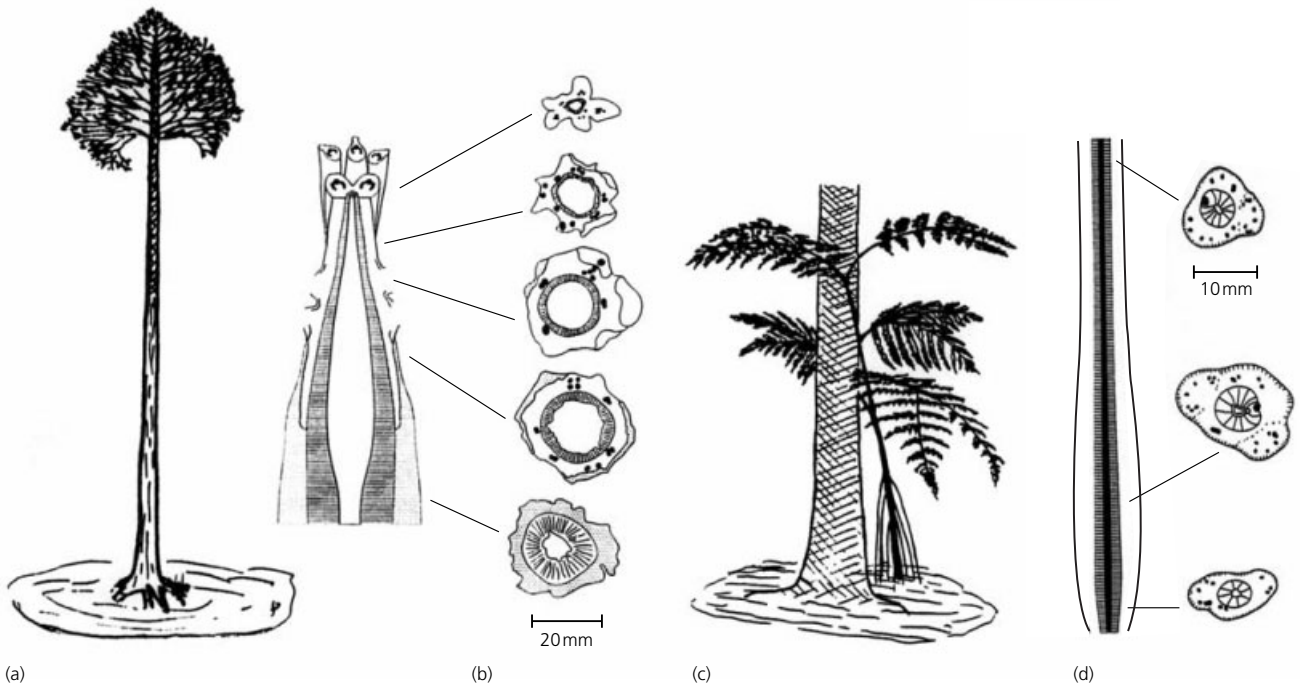

Fig. 4.1.3.3 Reconstruction of the growth form of some biomechanically analysed woody Palaeozoic plants. (a) Reconstruction of *Diaphorodendron vasculare*, a self-supporting tree with a maximum height of 12–20 m. (b) Diagram with schematic cross-sections of a self-supporting young branch of *Pitus dayi*, probably belonging to a tree-like '*Pitus*-plant'. (c) Reconstruction of *Lyginopteris oldhamia*, a semi-self-supporting plant. (d) Diagram with schematic cross-sections of a semi-self-supporting stem segment of *Calamopitys* sp. (a, Redrawn from DiMichele 1981, *Palaeontogr.* **B175,** 85–125.)

growth form of small-bodied herbaceous or pseudoherbaceous fossil plants that lack significant secondary growth. Analyses of extant small-bodied plants without secondary growth have shown that the axial diameters do not necessarily reflect the age of a section or position on the plant (Rowe and Speck 1998; Speck and Rowe 1999b). Therefore, growth form cannot be inferred reliably from general data but depends on the availability of positional information.

In addition to analysing overall growth forms, the biomechanical method also permits calculations of the contributions made by different stem tissues to flexural stiffness. This has been done for the plants mentioned above as well as for a number of small-bodied Early and Middle Devonian land plants. Such analyses have been used to infer the mechanical importance of parenchyma (turgor-stabilized basic tissue of plants), vascular systems (conducting tissue comprising xylem and phloem), and hypodermal steromes (strengthening tissue, one to several cell layers thick beneath the epidermis) for support among early vascular land plants (Speck and Vogellehner 1994; Bateman *et al.* 1998). The data suggest that many of the earliest land plants with cylindrical axes relied on turgescent parenchyma to maintain an upright posture, and that size and branching were therefore limited. Plants with turgor-stabilized axes, such as *Aglaophyton major*, *Rhynia gwynne-vaughanii*, *Horneophyton lignieri*, *Zosterophyllum rhenanum*, *Asteroxylon mackiei*, and *Drepanophycus spinaeformis* (Fig. 4.1.3.4a–f), were confined to habitats with continual and sufficient water supply and high humidity. With the colonization of water-limited habitats, hypodermal steromes became the most important stabilizing tissues, as in *Psilophyton dawsonii*, *Gosslingia breconensis*, and *Zosterophyllum llanoveranum* (Fig. 4.1.3.4g,h). In practically all of these early plants, the stele was of no importance for direct mechanical support, neither in the earlier turgor systems nor in later forms with hypodermal sterome. The only exception was the Middle Devonian protolepidodendralean lycopsid *Leclercqia complexa* (Fig. 4.1.3.4i) in which the stele and hypodermal sterome both contributed significantly to the mechanical stability of the stem. Studies of the type of support, maximum height and branching frequency, and mechanical significance of individual tissues have provided important insights into the ecology of early land plants and constraints on their evolution (Bateman *et al.* 1998).

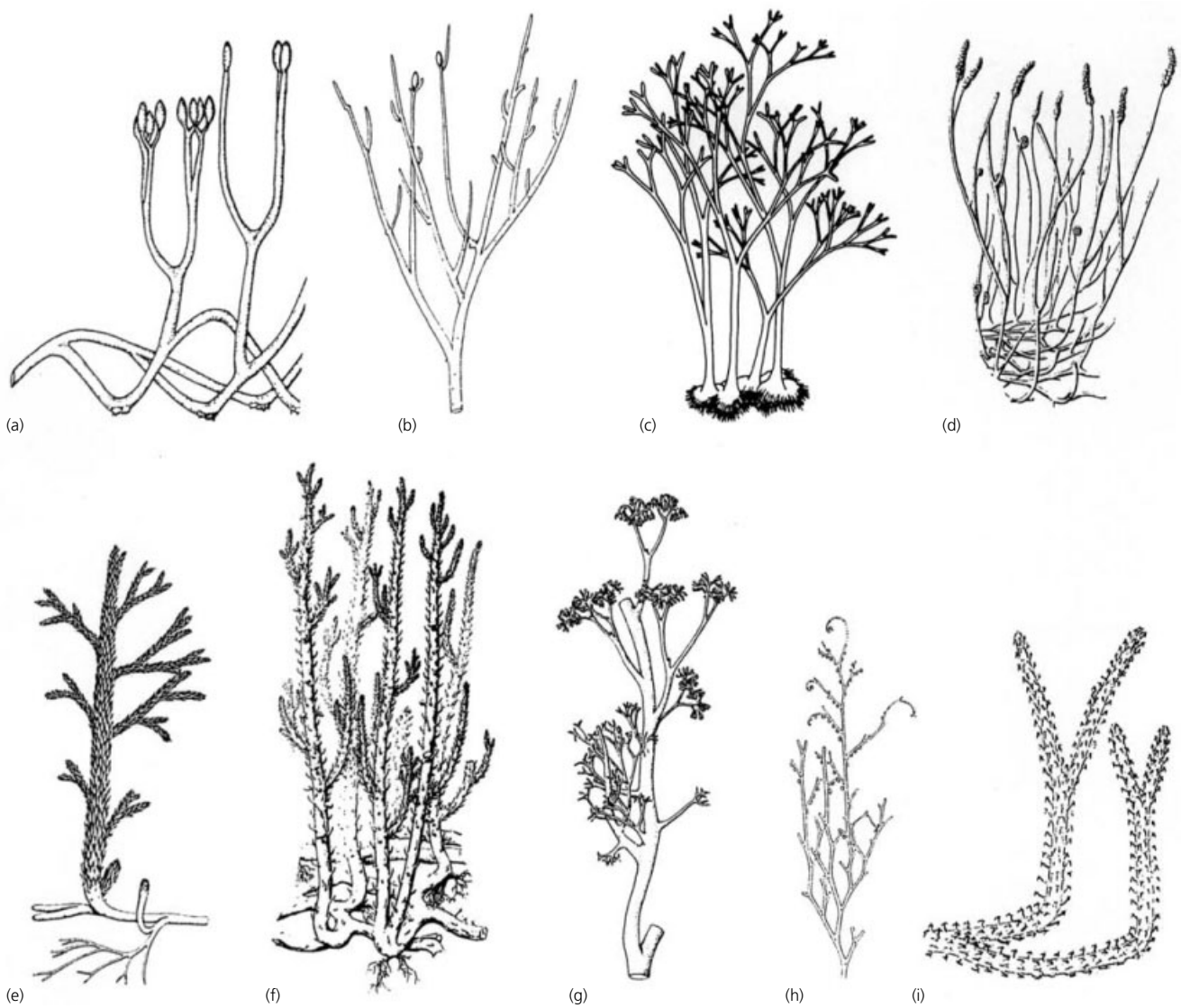

Fig. 4.1.3.4 Reconstruction of the growth form of some biomechanically analysed Early and Middle Devonian land plants: (a–f) plants with turgor-stabilized axes; (g,h) plants with axes predominantly stabilized by hypodermal steromes. (a) *Aglaophyton major*. (b) *Rhynia gwynne-vaughanii*. (c) *Horneophyton lignieri*. (d) *Zosterophyllum rhenanum*. (e) *Asteroxylon mackiei*. (f) *Drepanophycus spinaeformis*. (g) *Psilophyton dawsonii*. (h) *Gosslingia breconensis*. (i) *Leclercqia complexa*, a plant where both the stele and the hypodermal sterome contributed a comparable amount to the mechanical stability of the upright stems. (a, From Edwards 1986, *Bot. J. Linn. Soc.* **93,** 173–204; b, from Edwards 1980, *Rev. Palaeobot. Palynol.* **29,** 177–188, with permission from Elsevier Science; c, from Eggert 1974, *Am. J. Bot.* **61,** 405–413; d,f, modified from Schweitzer 1990, *Pflanzen erobern das Land*; e, from Stewart 1983, *Palaeobotany and the evolution of plants*; g, from Banks *et al.* 1975, *Palaeontogr. Am.* **8,** 77–127; h, from Edwards 1970, *Phil. Trans. R. Soc. Lond. B* **258,** 225–243; i, from Bonamo *et al.* 1988, *Bot. Gaz.* **149,** 222–239, with permission from The University of Chicago Press.)

References

Bateman, R.M., Crane, P.R., DiMichele, W.A., Kenrick, P.R., Rowe, N.P., Speck, T. and Stein, W.E. (1998) Early evolution of land plants: phylogeny, physiology, and ecology of the primary terrestrial radiation. *Annual Review of Ecology and Systematics* **29**, 263–292.

Rowe, N.P. and Speck, T. (1998) Biomechanics of plant growth forms: the trouble with fossil plants. *Review of Palaeobotany and Palynology* **102**, 43–62.

Speck, T. (1994) A biomechanical method to distinguish between self-supporting and non self-supporting fossil plants. *Review of Palaeobotany and Palynology* **81**, 65–82.

Speck, T. and Rowe, N.P. (1994) Biomechanical analysis of

Pitus dayi: early seed plant vegetative morphology and its implications on growth habit. *Journal of Plant Research* **107**, 443–460.

Speck, T. and Rowe, N.P. (1999a) Biomechanical analysis. In: T.P. Jones and N.P. Rowe, eds. *Fossil plants and spores: modern techniques*, pp. 105–109. Geological Society of London.

Speck, T. and Rowe, N.P. (1999b) A quantitative approach to analytically defining size, form and habit in living and fossil plants. In: M. Kurmann and A.R. Hemsley, eds. *The evolution of plant architecture*, pp. 447–479. Royal Botanic Gardens, Kew.

Speck, T. and Vogellehner, D. (1994) Devonische Landpflanzen mit und ohne hypodermales Sterom—Eine Biomechanische Analyse mit Überlegungen zur Frühevolution des Leit- und Festigungssystems. *Palaeontographica B* **233**, 157–227.

4.1.4 Sessile Invertebrates

W.I. AUSICH and D.J. BOTTJER

Introduction

The ocean floor offers a myriad of benthic habitats differentiated by numerous parameters—physical, chemical, and biological. Some processes and attributes of the environment only establish basic conditions, whereas others are limiting factors. Some have remained relatively constant through history, some have varied through time and space (i.e. penetration of sunlight and mineralogical composition of substrata), and others have undergone secular change through geological history (i.e. predation pressure and tiering). Metazoans and other larger life forms evolved principally in benthic habitats during the Proterozoic, and the late Proterozoic–early Palaeozoic metazoan radiation was intimately linked to the resources, conditions, and limitations at and near the sediment–water interface.

Sessile invertebrates are treated here as those in which adult organisms are permanently affixed (e.g. cemented oysters and encrusting bryozoans), passively affixed through a lack of mobility (e.g. free-living strophomenid brachiopods and inoceramid bivalves), or effectively sessile despite an ability to move episodically (e.g. pectinate bivalves and isocrinid crinoids). In addition, many organisms that are generally considered vagile, such as suspension-feeding ophiuroids and some deposit-feeding bivalves, are effectively sessile where feeding is concerned.

History of tiering

Tiering is the vertical subdivision of space by organisms within a community, and the processes responsible for this organization include space, resources, and constructional constraints (Ausich and Bottjer 1982). The Phanerozoic history developed here is for suspension-feeding communities on soft substrata, non-reef, shallow subtidal, and epicontinental environments. The tiering history represents the maximum characteristic tiering heights and depths within tier subdivisions. Clearly, not all communities display the maxima, and taller organisms and deeper burrows did exist.

Later studies refined the history and defined the occupants of tiers (e.g. Bottjer and Ausich 1986). A distinction was made between primary and secondary tierers, where primary tierers are organisms whose bodies are in contact with the sediment–water interface and secondary tierers are organisms that live either attached to primary epifaunal tierers or in the burrows of infaunal primary tierers (Bottjer and Ausich 1986). Tiering is now one of the primary ways in which palaeoecologists understand ancient epifaunal and infaunal communities. This contribution presents a revised history of primary tiering among suspension feeders on soft substrata (Fig. 4.1.4.1).

Expansion of larger organisms during the Proterozoic

The first, larger multicellular benthic organisms were the Ediacaran biota that evolved and radiated during the late Proterozoic. Regardless of the affinities of these organisms, the Ediacaran biota represents the initial establishment of soft-substrata benthos into vertically differentiated epifaunal tiers. Three epifaunal tier subdivisions are recognized: 0 to +5 cm, +5 to +20 cm, and +20 to +75 cm. The characteristic maximum height of late Proterozoic tiers was +75 cm, but as more data become available a higher level may be required (Jenkins 1992). Examples of occupants of these tiers from Ediacaran assemblages of South Australia include: 0 to +5 cm tier, *Arkarua*; +5 to +20 cm tier, *Glaessnerina*; and +20 to +75 cm tier, *Charniodiscus* (see Jenkins 1992).

Unfortunately, this well-developed ecological structure does not help to differentiate between competing hypotheses for the affinities of this biota. If erect forms, such as *Charniodiscus*, were cnidarians, then tiering would have enabled differentiation of suspension-feeding levels, as was common throughout the Phanerozoic. Alternatively, tiering within this biota could have been a function of competition for space or positioning for photoreception.

Duality of Cambrian communities and Cambrian tiering

Analysis of Ediacaran organisms extends tiering into the Proterozoic and, depending on their affinities, indicates either a continuity or discontinuity between tiering in

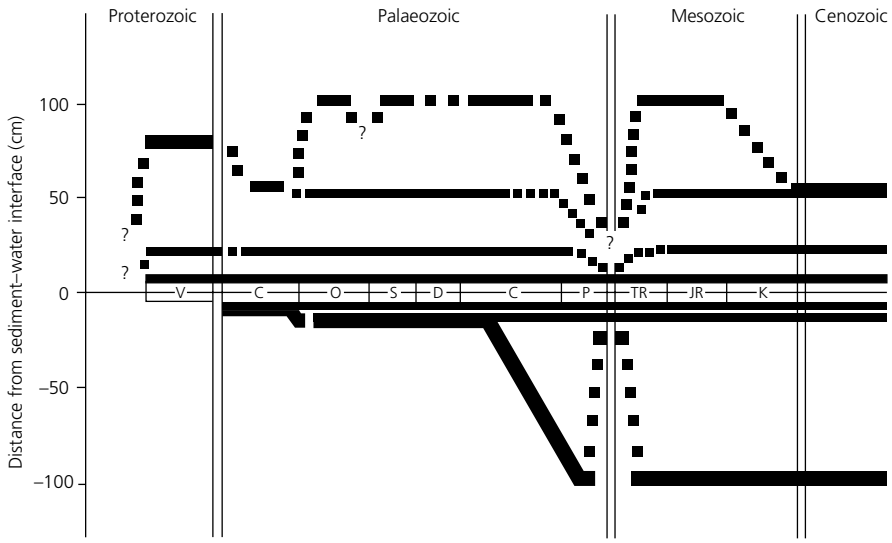

Fig. 4.1.4.1 Tiering history among soft-substrata suspension-feeding communities from the late Proterozoic through the Phanerozoic. Zero on the vertical axis indicates the sediment–water interface; the heaviest lines indicate maximum levels of epifaunal or infaunal tiering; other lines are tier subdivisions. Solid lines represent data, and dotted lines are inferred levels.

the soft-bodied Ediacaran biota and that of skeletonized Phanerozoic fauna. Ediacaran-type fronds occurred during the Early Cambrian and extended into the Middle Cambrian (Conway Morris 1993; Jensen *et al.* 1998). Thus, Phanerozoic metazoan tiering may extend back into the late Proterozoic, in which case tiering of skeletonized forms filled an existing epifaunal structure of earlier metazoans. Alternatively, a decline in Ediacaran tiering may reflect a concomitant rise in metazoan tiering.

It appears that late Proterozoic tiers evolved into those of the Early Cambrian, following which higher levels decreased and merged with tiering of skeletonized communities by the Middle Cambrian. Sponges are among the highest epifaunal suspension feeders during the Middle Cambrian. At this time it is unclear whether the tiering pattern is (1) the result of an evolutionary decline and a true reduction of Proterozoic tier heights, or (2) the closing of a taphonomic window and thus simply the result of poor preservation (Jensen *et al.* 1998).

Typical Middle Cambrian skeletonized, suspension-feeding communities had a 0 to +5 cm tier filled by brachiopods, sponges, echinoderms, and various other organisms. The +5 to +10 cm tier was occupied by erect echinoderms (such as eocrinoids) and sponges, and the +10 to +50 cm tier was probably only occupied by sponges.

Expansion of epifaunal tiering during the Ordovician

The +50 cm intermediate tier was immediately occupied by stalked echinoderms when Ordovician suspension-feeding faunas diversified. Discoveries of Ordovician pelmatozoan Lagerstätten demonstrated that epifaunal tier heights reached a maximum during the Middle Ordovician, when the length of camerate crinoid columns exceeded 90 cm. Middle and Late Ordovician crinoids maintained the +100 cm tier.

A typical Middle Ordovician community would have had a 0 to +5 cm tier filled with sponges, corals, bryozoans, articulate brachiopods, bivalves, rhombiferan echinoderms, diploporan echinoderms, and crinoids. The +5 to +20 cm tier was filled with sponges, corals, bryozoans, rhombiferan echinoderms, diploporan echinoderms, crinoids, and graptolites. The +20 to +50 cm tier was filled with diploporan echinoderms and crinoids, and the +50 to +100 cm tier would have been occupied only by crinoids. This highest tier level was undoubtedly reduced due to end-Ordovician extinctions, but it recovered rapidly during the Early Silurian to the +100 cm level and was maintained throughout the remainder of the Palaeozoic, except for the end-Permian event.

Terminal Palaeozoic extinctions and their impact on tiering

Evidence for infaunal tiering during the Early Triassic indicates that it was strongly affected by the end-Permian mass extinction (e.g. Schubert and Bottjer 1995), as was epifaunal tiering (Ausich and Bottjer 1982) (Fig. 4.1.4.1). Extinction-mediated low levels of infaunal and epifaunal tiering persisted for much of the Early Triassic (e.g. Schubert and Bottjer 1995), which constitutes the unusually long recovery interval for this mass extinction. Deep burrower refuges from the effects of this mass extinction may have been preferentially located in the high northern latitudes; evidence for Early Triassic deeper infaunal tiering first appears in Spitsbergen (Wignall *et al.* 1998).

Discussion

Analysis of tiering organization is an instructive way to investigate the physical structure and resource subdivision within benthic communities. It can be applied to suspension feeders on soft substrata, as described here, but it is also important for understanding deposit-feeding communities and hardground communities. Tier subdivisions are not necessarily rigid, but they are chosen as descriptions of the observed natural community organization. It may be appropriate to identify fewer or more tier subdivisions in particular communities.

A working hypothesis of characteristic tiering trends is shown in Fig. 4.1.4.1. Tiering within benthic communities was first established by the late Proterozoic Ediacaran biota. The selection pressures that prompted tiering (i.e. resource partitioning) were probably also at least partially responsible for diversification of body plans during this earliest evolution of benthic metazoans. Similarly, tiering and resource partitioning processes were undoubtedly important in shaping the characters of organisms during the Ordovician diversification. The Proterozoic–Phanerozoic transition in Fig. 4.1.4.1 is the interval most likely to require revision, because palaeontologists are still learning much and debating the biology and ecology of organisms from this time. Apparently elements of the Ediacaran biota persisted into the Cambrian, so tiering of those organisms continued. Radiation of the skeletonized fauna during the latest Proterozoic and Cambrian did not emphasize suspension feeding. Cambrian tiering heights were apparently lower than during the Proterozoic and were filled with Proterozoic holdovers, new metazoans, or both. Through the Middle and Late Cambrian, suspension feeders diversified to occupy more fully the reduced tiers of that time, and finally, the Ordovician radiation produced a tiering structure that remained stable, except for extinction-mediated perturbations, until the Cretaceous.

The 'Big Five' Phanerozoic mass extinctions had a major impact on tiering structure (Fig. 4.1.4.1). End-Ordovician extinctions reduced the maximum heights of epifaunal tiers. The end-Permian extinctions had the greatest consequences for tiering, with both epifauna and infauna being strongly affected. The end-Permian crisis was the only interval during the Phanerozoic in which a decrease in infaunal tiering occurred. These extinction-mediated tiering decreases reflect a significant loss of taxa during these biotic crises. It is probable that other extinction intervals also reduced tiering, but either the degree of reduction was too low or tiering recovery was too rapid for the changes to be evident in the fossil record.

References

Ausich, W.I. and Bottjer, D.J. (1982) Tiering in suspension-feeding communities on soft substrata throughout the Phanerozoic. *Science* **216**, 173–174.

Bottjer, D.J. and Ausich, W.I. (1986) Phanerozoic development of tiering in soft substrata suspension-feeding communities. *Paleobiology* **12**, 400–420.

Conway Morris, S. (1993) Ediacaran-like fossils in Cambrian Burgess Shale-type faunas of North America. *Palaeontology* **36**, 593–635.

Jenkins, R.J.F. (1992) Functional and ecological aspects of Ediacaran assemblages. In: J.H. Lipps and P.W. Signor, eds. *Origin and early evolution of the Metazoa*, pp. 131–176. Plenum Press, New York.

Jensen, S., Gehling, J.G. and Droser, M.L. (1998) Ediacara-type fossils in Cambrian sediments. *Nature* **393**, 567–569.

Schubert, J.K. and Bottjer, D.J. (1995) Aftermath of the Permian–Triassic mass extinction event: paleoecology of Lower Triassic carbonates in the western USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* **116**, 1–39.

Wignall, P.B., Morante, R. and Newton, R. (1998) The Permo-Triassic transition in Spitsbergen: $\delta^{13}C_{org}$ chemostratigraphy, Fe and S geochemistry, facies, fauna and trace fossils. *Geological Magazine* **135**, 47–62.

4.1.5 Trilobites

B.D.E. CHATTERTON

Introduction

Trilobites were abundant and diverse for almost 300 million years, during the Palaeozoic Era. They are notable because they were active, sighted animals. Since they had calcite exoskeletons and moulted regularly, ontogenies from larva to adult are known for many species. Their similarities to modern arthropods (horseshoe crabs and isopods) and the rocks they occur in are used to hypothesize how they lived. All trilobites were marine. They ranged from shallow, nearshore environments to deep environments, below the photic zone.

Ontogeny and life cycles

Trilobites have been described from possible eggs, from calcified larvae where cephalon and pygidium are fused (protaspides), through stages where cephalon and pygidium separate and segments are released into a thorax (meraspides), and finally to mature stages where growth continued but no segments were released (holaspides; Chatterton and Speyer 1997).

Trilobite larvae occur in a number of shapes and sizes. Some underwent radical metamorphosis during early ontogeny, associated with a change from planktic to benthic life modes. Trilobites with several planktic instars show reduced latitudinal spread at the onset of glaciation during the Middle Ordovician, and then poor survivorship during the latest Ordovician mass extinction. Survivorship was higher among trilobites with a single or no planktic instar. This relationship suggests that conditions in the planktic realm were difficult for trilobites for much of the year. Perhaps extended seasonal shortages of food, cool temperatures and/or the presence of floating ice during episodes of more extreme glaciation adversely affected planktic organisms.

Diversity, biofacies, and associations

Trilobites were most abundant and diverse during the Cambrian and Ordovician periods. Alpha diversities of trilobites changed little from the Late Cambrian through the Ordovician (Westrop and Adrain 1998), and what appears to be a decline is a process of dilution (through increased abundance and diversities of other groups, such as brachiopods, molluscs, and bryozoans). It has been suggested that diversities of trilobites with smooth vs. rough surface sculptures were affected differentially by the abundance and diversity of predators with suction devices for grasping (cephalopods and starfish). The radiation of jawed fishes in the Devonian apparently caused a reduction of trilobite diversity that preceded the demise of trilobites by 100 million years.

During the Ordovician, shallow, warm-water biofacies show low diversities of trilobites; diversities increase in deeper shelf to slope facies, and they decline again in even deeper waters. This has been related to deposit-feeding habits among many trilobites. Some features that vary in relation to water depth or proximity to shoreline are shown in Fig. 4.1.5.1. Typically, three to five trilobite biofacies are recognized in a transect from shore to continental slope (see Fig. 4.1.5.2).

Autecology and functional morphology

Eyes

Trilobite eyes are composed of calcite. Numerous lineages show convergent eye loss, associated with living below the photic zone. Hypertrophied (large) eyes, particularly those with wide fields of view, are associated with pelagic taxa (Fortey 1985). Size of eyes, size and number of lenses, and shape and orientation of visual surfaces are clues to modes of life. The number of lenses determined visual acuity, and the size of lenses was a factor in determining detectable light levels. Trilobites with well-developed eyes were usually able to enroll effectively. A detection system, such as vision, is a necessary precursor to evolving a protective strategy, such as enrolling or escaping.

Two trilobites from the Ordovician (Llanvirn) near St Petersburg, Russia, have eyes at the ends of long stalks. While one of them, *Asaphus kowalewskii*, is comparatively smooth and may have been able to burrow, it is doubtful whether the other, *Cybele bellatula*, which has a well-developed sculpture of tubercles and long marginal spines on the thoracic segments, was also able to burrow into the substrate. Perhaps these eyes were stalked to see above forests of organisms growing on the sea floor, or above clouds of mud stirred up by the trilobites while they were feeding.

Shell thickness, enrolment, and caeca

A relationship between an onshore-offshore environmental gradient and shell thickness has been demonstrated for Lower Ordovician trilobites. Offshore trilobites have thinner shells. This pattern is known for such other invertebrates as brachiopods and presumably is related in part to differences in the energy of the environment.

Trilobites of shallow shelf environments are commonly found enrolled. Enrolment is more common

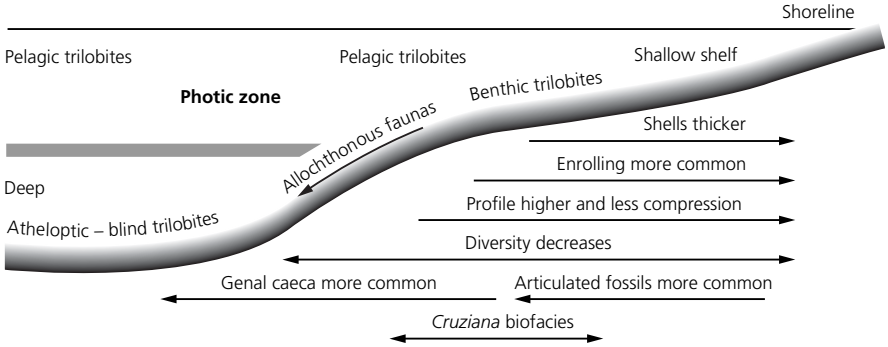

Fig. 4.1.5.1 Factors that vary among trilobites in relation to water depth or proximity to shore. 'Profile' refers to the degree of dorsoventral inflation of trilobites. 'Compression' refers to the amount of diagenetic flattening as a result of dewatering of clay-rich sediments. 'Diversity' refers to trilobite alpha diversities, in different communities.

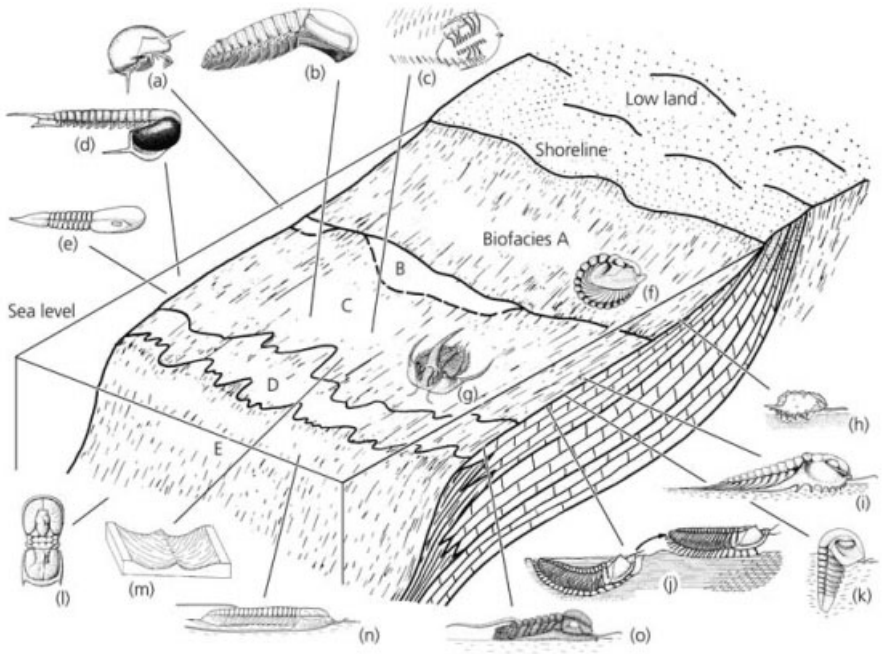

Fig. 4.1.5.2 Trilobites and trilobite traces. The biofacies shown (A–E) are hypothetical, based upon Middle Ordovician trilobite biofacies from northern Laurentia. (a) Planktic protaspis of *Isotelus* (1 mm long); (b) adult *Remopleurides* (20 mm long); (c) walking traces, *Dimorphichnites* (width variable); (d) planktic *Opipeuter* (30 mm long); (e) nektobenthic *Parabarrandia* (100 mm long); (f) enrolled *Flexicalymene* (15 mm diameter); (g) outstretched *Acidaspis* (18 mm across); (h) benthic, adult-like protaspis of *Physemataspis* (0.5 mm long); (i) 'snow-shoe' supported *Exallaspis* (Silurian, 14 mm long); (j) burrowing and walking *Neseuretus* (25 mm long); (k) burrowing *Panderia* (8 mm long); (l) deep benthic, blind *Machairagnostus* (5 mm long); (m) short segment of burrowing trail *Cruziana* (width variable); (n) deep benthic olenid *Balnibarbi* (110 mm long); (o) benthic *Dimeropyge* (10 mm long). (Illustrations adapted and redrawn from original sources.)

in Ordovician and younger strata than it is in the Cambrian.

Several authors have noted a relationship between fine anastomosing ridges in the pleural regions (genal caeca), and trilobites dwelling in deep, quiet environments. These caeca may have been secondary respiratory devices, important where oxygen levels were low (Jell 1978).

Spines

Spines have been considered to be defensive structures, 'snow-shoe' supporting devices, or to fulfil certain hydrodynamic functions in swimming. Elongate spines would have generated enough frictional drag to render swimming inefficient. The number of trilobites with arrays of spines reached an acme during the Early and Middle Devonian, when jawed fishes preyed upon them. Blunt spines on the front of the cephalon may have been used for digging (Whittington 1992).

Burrows

Some trilobites formed burrows, which they entered, forwards or backwards, at varying angles to the surface. The most common trilobite traces are *Cruziana* and *Rusophycus*. Some ichnospecies can be associated with trilobite species. Other species of the same ichnogenera, however, were made by other arthropods (Whittington 1992). The burrowing trilobites usually lack strong external sculpture, and often have shallow furrows in their exoskeletons.

Pelagic trilobites

There is a convincing functional morphological case that some telephinid and cyclopygid trilobites were pelagic (Fortey 1985). These planktic trilobites apparently descended to the sea floor to moult (see Whittington 1992). Flume tank experiments suggest that *Parabarrandia* may have been nektonic, based on its streamlined form (Fortey 1985).

Hypotheses that small or spinose trilobites were pelagic or epipelagic are usually unconvincing when functional morphology, taphonomy, and stratigraphic distributions are considered. Neither agnostids nor most other small adult trilobites were pelagic. Facts suggesting that agnostids were not pelagic, but small

deep-water benthic animals, are many: they are blind; they are not particularly thin shelled; they are often unevenly distributed stratigraphically through sections; and when not enrolled, they have planar ventral surfaces. In the Middle Cambrian Wheeler Shale of Utah, most of the agnostids are articulated, with convex surfaces upward in what appears to be life position, and sometimes on the same bedding planes as articulated benthic trilobites like *Elrathia kingi* (Levi-Setti 1993). Arguments based on the form of the appendages of small agnostids, preserved in the orsten deposits of Sweden, are equivocal.

Moulting

Many trilobites moulted individually. Other trilobites moulted in groups or their moults accumulated at particular sites. Aggregations of moults of leaf-like scutelluines are found in pockets in reefs, particularly the Devonian reefs of Bohemia and Morocco.

Mature trilobites moulted on or in the substrate. Many examples have been found of single-species aggregations of mature trilobites, apparently trapped by storm deposits. It has been suggested that these gatherings were for mutual protection during moulting, perhaps followed by reproduction. Collections of Silurian *Acernaspis* from Anticosti Island include specimens with series of moults in burrows. One specimen has an L-shaped row of at least 25 partly articulated moults, lying as much as three deep in what may be a burrow.

Articulated and disarticulated trilobites are commonly found in the living chambers of cephalopods, suggesting that they entered the shell after death of the cephalopod, to scavenge, moult, or hide.

Food

Trilobites were predators on small animals, or scavengers, or ingesters of sediment containing organic particles. They were able to dig into the substrate to search for food or hide (Whittington 1992). Evidence for feeding habits ranges from trace fossils to exceptionally preserved examples that show the appendages and/or alimentary tract. The best 'smoking guns' are Swedish Lower Cambrian burrows, *Rusophycus dispar*, which terminate worm traces (Jensen 1990)—evidence of trilobites preying on worms.

Trilobites as food

Trilobite predators included Cnidaria, Cephalopoda, other Arthropoda (*Anomalocaris*, eurypterids, phyllocarids, stomatopods), jawed fishes, Asterozoa, and polychaete worms. Numerous examples of non-lethal injuries to trilobites have been described, some made by predators and parasites, others occurring during moulting. Most of these healed injuries are in the pleural regions. In only a few cases can the injuries definitely be attributed to failed attacks by predators.

References

Chatterton, B.D.E. and Speyer, S.E. (1997) Ontogeny. In: R.L. Kaesler, ed. *Treatise on invertebrate paleontology. Part O (Arthropoda 1, revised).* Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas.

Fortey, R.A. (1985) Pelagic trilobites as an example of deducing the life habits of extinct arthropods. *Transactions of the Royal Society of Edinburgh, Earth Sciences* **76**, 219–230.

Jell, P.A. (1978) Trilobite respiration and genal caeca. *Alcheringa* **2**, 251–260.

Jensen, S. (1990) Predation by Early Cambrian trilobites on infaunal worms—evidence from the Swedish Mickwitzia Sandstone. *Lethaia* **23**, 29–42.

Levi-Setti, R. (1993) *Trilobites,* 2nd edn. University of Chicago Press, Chicago.

Westrop, S.E. and Adrain, J.M. (1998) Trilobite alpha diversity and the reorganization of Ordovician benthic marine communities. *Paleobiology* **24**, 1–16.

Whittington, H.B. (1992) *Trilobites*. Boydell Press, Bury St Edmunds, England.

4.1.6 Trackways—Arthropod Locomotion

S.J. BRADDY

Introduction

The arthropods have an extensive fossil record and today constitute the most abundant and diverse group of animals on land. Their fossilized trackways and trails provide important data in studies of arthropod evolution and contribute towards our understanding of their diversity and temporal, geographical and palaeoenvironmental distribution (including the history of terrestrialization). As trace fossils are preserved *in situ*, they represent a reliable record of the presence of an animal in a particular environment. As different conditions are required for the preservation of trace fossils and body fossils, traces may extend the stratigraphic range of certain groups. The myriapods, for example, are known from trackways much older than their earliest body fossils (Johnson *et al.* 1994).

More importantly, fossil trackways represent 'snapshots' of the behaviour of extinct arthropods. It is possible to reconstruct the walking techniques of fossil arthropods from modern analogues; investigations of living arthropods may allow the producer, behaviour, and preservational circumstances of fossil trackways to be identified. Certain groups (e.g. eurypterids and arthropleurids), however, have no extant equivalent; while their locomotory capabilities may be investigated through functional studies and biomechanical modelling, an analysis of their trackways (assuming the producer can be determined) can provide more reliable evidence for their walking techniques.

Gaits

Arthropods walk by combining *promotor–remotor* and *levator–depressor* movements of their legs (Manton 1977). The *period*, or time taken to complete one *step cycle* (i.e. one complete promotor–remotor swing) is divided into the *protraction period* (p), or forward (recovery) stroke, and the *retraction period* (r), or backward (propulsive) stroke. Arthropods regulate the movement of their legs, in order to avoid interference between them and walk efficiently, according to three parameters: the *gait* (i.e. $p:r$ ratio, usually expressed as a proportion of 10), the *opposite phase difference* (the proportion of the step cycle that the right legs move after the left legs), and the *successive phase difference* (the proportion of the step cycle that a leg moves in advance of the leg in front).

Understanding the functional mechanics of trackway production is fundamental to interpreting the producer's behaviour (for terminology, see Fig. 4.1.6.1). It is possible to reconstruct the gait of the producer, although this requires that the backward stroke distance (i.e. distance covered by the distal part of the leg during the propulsive stroke) be known. This may be assessed by functional analysis of body fossils (Briggs *et al.* 1979). The gait ratio ($p:r$) out of 10 (i.e. $p=10-r$) may be calculated according to the equation:

$$r = \left(\frac{\text{backstroke}}{\text{stride}}\right) \times 10 \qquad (1)$$

assuming that the stride can be deduced from the trackways. Arthropods are not constrained to walk in only one way, and trackways may evidence the range of gait parameters that were used. Arthropods employ different walking techniques in response to functional requirements (e.g. a myriapod pushing through vegetation will use a lower geared gait than when it is running over open ground: Briggs *et al.* 1979).

Determination of producer

It is not generally possible to identify the producer of a trackway, unless the animal responsible is preserved at the end of it. As trace fossil taxa (ichnotaxa) are based solely on the trace morphology, rather than the identity of the producer, different types of arthropod can produce the same trackway ichnotaxon, while a single individual can produce many different ichnotaxa depending on behaviour (walking technique) or preservation (substrate conditions). Trackways may show preservational grades (Johnson *et al.* 1994), or taphoseries, converging on similar ichnotaxa. *Mirandaichnium*, for example, rep-

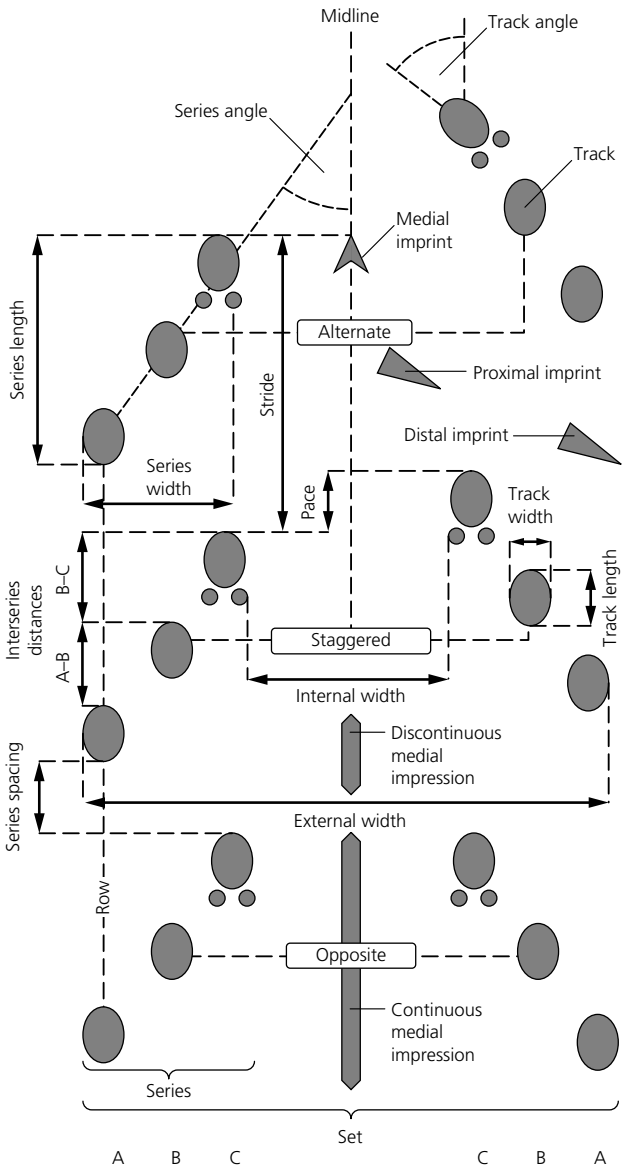

Fig. 4.1.6.1 Trackway terminology, based on a hypothetical trackway resembling *Palmichnium kosinskiorum*. Terminology after Trewin (1994) with modifications: 'pace' denotes longitudinal distance between opposing tracks, as in vertebrate ichnology, not distance between tracks in same series (here termed 'interseries distances', e.g. A–B, B–C).

resents a preservational grade where wet sediment adheres to the underside of an animal and is dragged in the direction of motion. Various different types of arthropod can produce this form under similar preservational conditions.

Analysis of trackways may reveal whether their producers were homopodous (i.e. walking limbs were of similar morphology) or heteropodous (i.e. walking limbs were of differing morphologies). The identity of the producer may also be inferred from a trackway by its size, morphology, co-occurrence with body fossils (in the same unit or contemporaneous strata), and the number of tracks (individual footprints) in a series. However, the series composition may not relate to the sequence of footfalls produced during one step cycle, or provide a reliable assessment of the number of walking legs. Preservational factors (e.g. undertrack fallout, where some tracks are not evident when the rock splits at a level beneath the surface upon which the trackway was produced) or behaviour (e.g. overprinting of tracks or missed steps) may conceal the evidence of some limbs. The action of currents or slopes may result in irregular or dimorphic trackways. Accessory imprints may reveal aspects of the producer's carapace or abdomen morphology. Medial impressions usually denote a tail spine and displacement of such impressions from the midline on turns may indicate a long tail, as in some *Paleohelcura* (scorpion) trackways. The curvature of trackways may also reflect the lateral flexibility of the producer.

Arthropod trackways may be used to detect evolutionary trends. They may reveal, for example, the biomechanics of early terrestrial arthropods. Aquatic arthropods tend to walk in-phase (i.e. the movement used in swimming). Terrestrial arthropods, on the other hand, tend to employ out-of-phase walking techniques because this confers greater stability. The development of a hanging stance, and plantigrade distal podomeres, also characterize terrestrial arthropods. Fossil trackways provide the only direct evidence for the functional transition from aquatic to terrestrial in different arthropod groups.

Trackways attributed to arthropod groups

Trilobites

Trilobite anatomy and behaviour can be inferred from their fossilized trackways and trails (Osgood 1970). These homopodous arthropods walked with anteriorly directed waves of leg movement, although their diversity of locomotory styles has produced a range of (sometimes intergradational) ichnotaxa: shallow ploughing (*Cruziana*, Fig. 4.1.6.2a), straight or slightly oblique walking (*Petalichnus*, Fig. 4.1.6.2b; *Asaphoidichnus*), strongly oblique (crab-like) walking (*Dimorphichnus*), or 'pulling' with only the stronger anterior appendages (*Allocotichnus*). The ichnogenus *Diplichnites* is frequently (incorrectly) applied to walking traces of trilobites; this ichnotaxon should be restricted to the trackways of arthropleurids (Briggs *et al.* 1979).

Other homopodous arthropods

Various trilobite-like trackways are so distinct that they are clearly the work of 'non-trilobites'. The trackway *Teratichnus*, attributed to aglaspidids (Osgood 1970), reveals that they walked in-phase with nine pairs of walking legs, and dragged the telson. The trackways of Burgess Shale arthropods are rare in the fossil record, but include *Angulichnus* (Fig. 4.1.6.2c), attributed to *Habelia optata* walking out-of-phase and leaving a continuous zigzag medial impression, made by its articulated telson.

Crustaceans

Crustacean trails from Lower Palaeozoic successions are often indistinguishable from those of trilobites. Mesozoic and brackish-freshwater occurrences of *Cruziana* are generally referred to *Isopodichnus* (although workers are divided over the validity of this approach). These trails (and isolated, *Rusophycus*-like bilobed resting traces) were possibly produced by notostracan or phyllopod crustaceans. Similarly *Merostomichnites* (unfortunately named, as it was assumed to have been produced by merostomes), widely recorded from Devonian–Mesozoic alluvial settings, was produced by homopodous, multilimbed (up to nine tracks per series) phyllopod crustaceans walking in-phase, in a straight or slightly oblique manner. The trackway *Siskemia elegans* was attributed to an unknown, crustacean-like, producer with three to five pairs of homopodous legs and paired rigid tail spines, walking (semi-swimming) in-phase in shallow water (Walker 1985). The Early Permian Dwyka (glacial) and Ecca (postglacial) deposits of South Africa yield various trackways (*Umfolozia*, Fig. 4.1.6.2d; *Maculichna*, *Tasmanadia*) attributed to homopodous syncarid or peracarid crustaceans employing various half-swimming, half-walking locomotory styles.

Myriapods and arthropleurids

The trackways (*Diplichnites*) and trails (*Diplopodichnus*) of myriapods provide some of the earliest (Ordovician) evidence for the activity of terrestrial arthropods (Johnson *et al.* 1994). These traces represent compound ichnotaxa reflecting variations in the consistency of the substrate. A myriapod (*Eoarthropleura*) trail from the Upper Silurian of Newfoundland was reconstructed

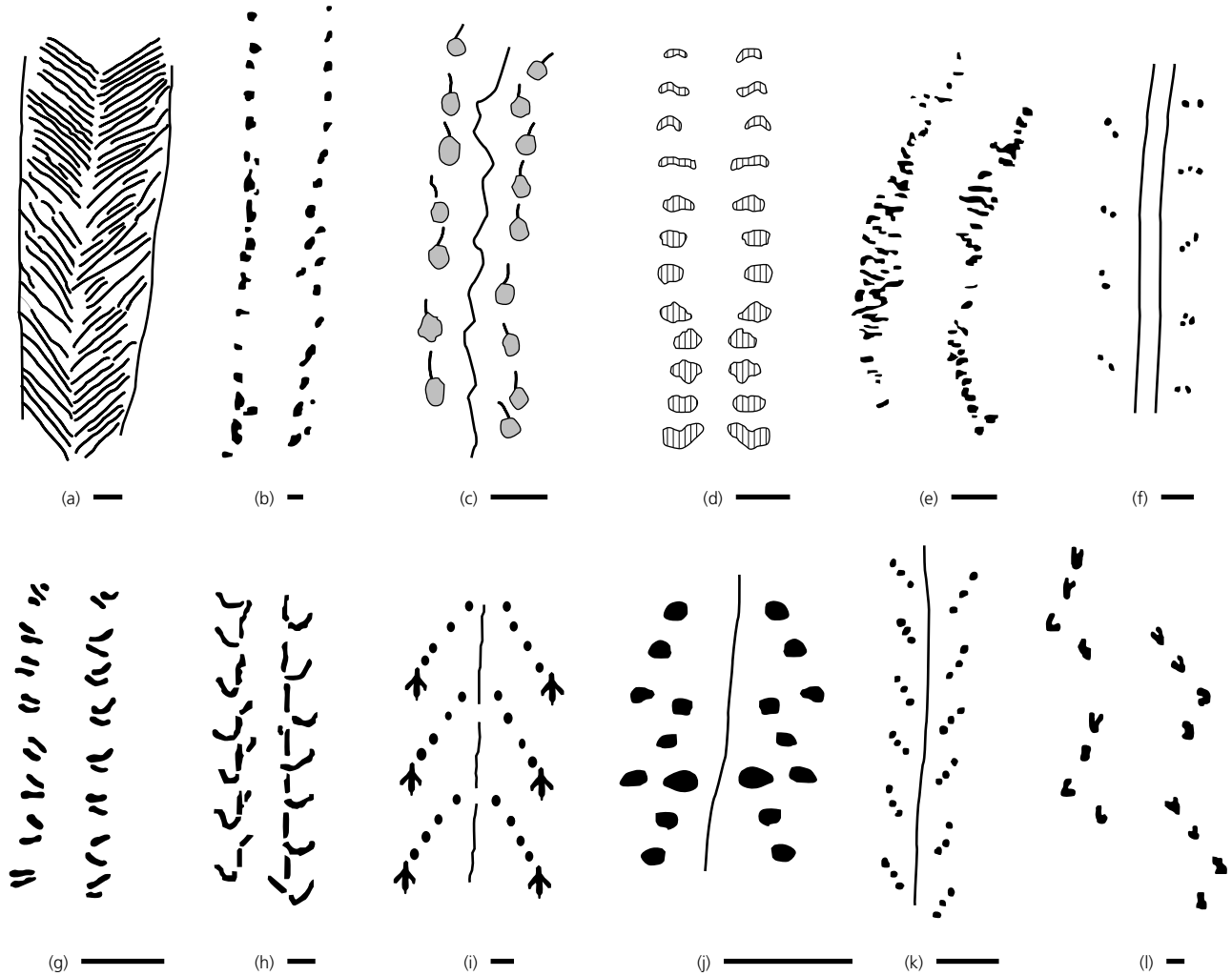

Fig. 4.1.6.2 Selected arthropod trackway ichnotaxa attributed to trilobites (a,b), *Habelia optata* (c), crustaceans (d), arthropleurids (e), insects (f–h), and chelicerates (i–l). (a) *Cruziana semiplicata*. (b) *Petalichnus brandenburgensis*. (c) *Angulichnus alternipes*. (d) *Umfolozia sinuosa*. (e) *Diplichnites cuithensis*. (f) *Siskemia bipediculus*. (g) *Permichnium voelckeri*. (h) *Lithographus hieroglyphicus*. (i) *Kouphichnium variabilis*. (j) *Palmichnium antarcticum*. (k) *Paleohelcura tridactyla*. (l) *Octopodichnus didactylus*. Scale bar = 1 cm (or 10 cm in e and j).

with a gait of 7.7 : 2.3 and a successive phase difference of 0.14, indicating that the producer was well adapted for subaerial locomotion. The trackways (*Diplichnites*, Fig. 4.1.6.2e) of arthropleurids (giant myriapod-like forms) are relatively common in late Lower Palaeozoic deltaic and fluvial successions, and by the Carboniferous they attain very large sizes. A large *Arthropleura* trackway from Arran, 36 cm wide, was reconstructed with a gait of 5.5 : 4.5, indicating that it was running over open ground (Briggs *et al*. 1979).

Insects

Insect trackways are scarce in the early Palaeozoic but may include some forms of *Siskemia* (e.g. *S. bipediculus*, Fig. 4.1.6.2f) from the Lower Devonian (Walker 1985), which show similarities to trackways of modern diplurans and thysanurans (e.g. see Manton 1977). Following a major radiation in the Carboniferous, the diversity of insect trackways increases considerably. Several trackway ichnotaxa (e.g. *Permichnium*, Fig. 4.1.6.2g) have been described from the Permian Rotliegendes ichnofauna of Germany (Walter 1983), which were probably produced by insects. In the middle of the nineteenth century Edward Hitchcock noted several trackways (e.g. *Lithographus*, Fig. 4.1.6.2h) from the Lower Jurassic Connecticut Valley ichnofauna which are attributable to insects. These trackways indicate

that the insects walked in a similar way to their modern relatives, predominantly using alternating gaits for maximum stability.

Chelicerates

Xiphosuran trackways (*Kouphichnium*, Fig. 4.1.6.2i) are well known from various settings but are particularly abundant in the Coal Measures. Spectacular examples of limulid trackways from the Solnhofen Limestone (Jurassic) are even associated with their (*Mesolimulus*) producer. These trackways reveal that xiphosurans walked in-phase with their five pairs of heteropodous walking legs, in a lurching-type gait, dragging the telson. The variety of their trackways, however, records various other locomotor styles (e.g. half-swimming).

Some of the largest arthropod trackways known from the fossil record are attributed to eurypterids. Most eurypterid trackways are rare, apart from *Palmichnium antarcticum* (Fig. 4.1.6.2j) which is known from several localities, sometimes in great abundance, and may indicate mass migrations across marginal environments, perhaps as part of the eurypterid life cycle. Eurypterids have been reconstructed using out-of-phase gaits, based on functional studies. Most of their trackways, however, show that these arthropods predominantly walked in-phase, like xiphosurans. Most eurypterids were not well adapted for walking on land. During amphibious excursions, the paddled forms employed an ungainly 'subaerial flop', hauling themselves forward with repeated in-phase lunges. Underwater, many eurypterids employed a half-swimming, in-phase 'subaqueous hop' manoeuvre. Stylonurids, on the other hand, were capable walkers, employing low-geared (e.g. 2:8), stable, in-phase gaits.

Arachnid trackways are rare in the early Palaeozoic. Scorpionid trackways (*Stiaria*) are known from the Old Red Sandstone of Scotland (Walker 1985). By the Lower Permian, the trackways of scorpions (*Paleohelcura*, Fig. 4.1.6.2k) and spiders (*Octopodichnus*, Fig. 4.1.6.2l) are widespread in both marginal and continental interior environments. Trackways similar to *Paleohelcura* (*Tarsichnus*) are also known from the Permian Rotliegendes ichnofauna in Germany (Walter 1983). The walking techniques employed by these arachnids were similar to those of their modern relatives. Out-of-phase gaits are evident from their alternate symmetry. Alternating tetrapod gaits (i.e. successive phase difference 0.5, opposite phase difference 0.5) would have provided the most efficient walking techniques, although variations in leg patterns (evident in the trackways) were presumably a response to functional requirements. Indeed, minor variations in walking techniques have often resulted in a profusion of names for trackways that modelling procedures, neoichnological investigations, and occasional intergrading specimens indicate were produced by the same animal.

References

Briggs, D.E.G., Rolfe, W.D.I. and Brannan, J. (1979) A giant myriapod trail from the Namurian of Arran, Scotland. *Palaeontology* **22**, 273–291.

Johnson, E.W., Briggs, D.E.G., Suthren, R.J., Wright, J.L. and Tunnicliff, S.P. (1994) Non-marine arthropod traces from the subaerial Ordovician Borrowdale Volcanic Group, English Lake District. *Geological Magazine* **131**, 395–406.

Manton, S.M. (1977) *The Arthropoda: habits, functional morphology and evolution*. Oxford University Press, Oxford.

Osgood, R.G. (1970) Trace fossils of the Cincinnati area. *Palaeontographica Americana* **6** (41), 281–444.

Trewin, N.H. (1994) A draft system for the identification and description of arthropod trackways. *Palaeontology* **37**, 811–823.

Walker, E.F. (1985) Arthropod ichnofauna of the Old Red Sandstone at Dunure and Montrose, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **76**, 287–297.

Walter, H. (1983) Zur Taxonomie, ökologie und biostratigraphie der ichnia limnisch-terrestrischer arthropoden des mitteleuropäischen Jungpaläozoikums. *Freiberger Forschungsheft C* **382**, 146–193.

4.1.7 Durophagy in Marine Organisms

R.B. ARONSON

Introduction

Durophagy is the consumption of prey that is protected by a hard skeleton. A wide diversity of invertebrate and vertebrate predators eat prey organisms that have biomineralized skeletons in modern marine environments. At one end of the spectrum, sea anemones feed opportunistically on dislodged mussels and sea urchins, which they swallow whole. Sea otters represent the opposite extreme, employing complex behaviours that include tool use to break open their molluscan prey. Two aspects of durophagous predation in the marine environment have received most attention from palaeontologists, primarily because the prey organisms preserve well and provide information about predator–prey encounters. The first is how temporal changes in skeleton-crushing by fish and crustaceans have affected the morphology

and abundance of their molluscan and echinoderm prey. The second is how drilling by predatory gastropods has changed over time.

Crushing predation

Many features of the skeletal design of Mesozoic and Cenozoic invertebrates are interpreted as adaptive consequences of durophagous predation (see Section 1.4.1). Shell-breaking teleosts, neoselachian sharks and rays, and decapod crustaceans diversified rapidly in nearshore environments beginning in the Jurassic (Vermeij 1987). Radiations of these predatory taxa were accompanied by, and are thought to have stimulated, the evolution of architectural defences in gastropods, bivalves, ammonoids, crinoids, and other marine invertebrates. In gastropods, defensive adaptations of the shell against increasing predation included increased spination and ribbing, decreased apertural width and increased dentition of the aperture, and tighter coiling of the shell about its central axis. Less extreme increases in the capabilities of predators and the defensive architectures of prey occurred in the mid-Palaeozoic, when the new predators were placoderm and chondrichthyan fish and the responding prey taxa included gastropods, nautiloids, brachiopods, and crinoids (Signor and Brett 1984). Going back to the beginning of the Phanerozoic, biomineralized skeletons themselves probably arose in the Early Cambrian in response to increasing predation.

Gradients in the morphology of prey skeletons occur at smaller scales as well. Phenotypic expressions of antipredatory architectures in gastropods are associated with shell-breaking predation in ecological time and space (reviewed by Aronson 1994). In a remarkable evolutionary example from a freshwater system, gastropods in Lake Tanganyika possess thickened, ornamented shells of the type normally found in marine systems. These endemic gastropods evolved over several million years in response to the unusually powerful crushing claws of an endemic crab species (West *et al.* 1991).

The frequency of sublethal shell damage (repaired cracks) in a gastropod population should be positively related to the effectiveness of that population's morphological defences in thwarting predatory attacks: increased sublethal damage should imply decreased levels of lethal shell-breaking (Vermeij 1987). The frequency of shell repair in gastropods generally increased beginning in the Mesozoic, apparently confirming the efficacy of newly acquired defensive morphologies. Nevertheless, interpreting patterns of shell repair can be problematic. Dead shells are often transported or destroyed and so cannot be evaluated for cause of death. In consequence, if only a few shells in the living population display sublethal damage, then either the attack rate is high and most attacks are lethal, or both the lethal and sublethal attack rates are extremely low. It has been claimed that the frequency of sublethal injuries provides an index of selection pressure for antipredatory features (Vermeij 1987). This assertion has been contested on the grounds that frequent predator–prey encounters are not necessary to select strongly for the evolution of antipredatory traits in prey. Thus, the significance of sublethal damage in molluscs is not always clear.

Drilling predation

The adaptations of predatory gastropods for drilling their molluscan prey also increased during the Mesozoic and Cenozoic. Shell thickness of prey and/or the frequency of drilled prey should have increased through time as a result (Kelley and Hansen 1996). The stereotypy of drilling should have increased as well: drill-holes in geologically younger shells should be more localized to profitable regions of the shell, and the positive correlation between predator and prey sizes should have become stronger with time. Temporal patterns of drilling predation are complex, however, and they do not always follow these predictions. One complication is that drilling gastropods were themselves subject to increasing levels of durophagy, including both shell-breaking by fish and crustaceans, and cannibalistic drilling.

Prey abundance

Increasing durophagous predation has not always resulted in the increased expression of defensive features in prey. A more direct consequence has been a decline in prey abundance. Dense populations of epifaunal, suspension-feeding ophiuroids (brittle stars; hundreds to thousands per m^2) are excluded from most modern coastal environments by predatory fish and decapods. Such dense populations persist in low-predation refuges in shallow water (Fig. 4.1.7.1), and they thrive in the deep sea. The primary predators on dense ophiuroid populations are slow-moving invertebrates such as asteroids (sea stars) (Fig. 4.1.7.1c).

Predatory fish and invertebrates usually attack the arms of ophiuroids before attacking the disc. Sublethal arm damage can therefore be used as an unambiguous, relative measure of the frequency of lethal as well as sublethal attacks. The proportion of ophiuroids bearing one regenerating arm or more is low in dense, epifaunal, living populations, indicating that predation pressure is low in their refuge habitats. Dense, fossil populations (Fig. 4.1.7.2) likewise exhibit low frequencies of sublethal damage, implying low predation pressure. The diversification of predators in the Mesozoic was accompanied by a marked decline in the occurrence of these dense, low-predation ophiuroid populations in shallow water (Aronson 1994).

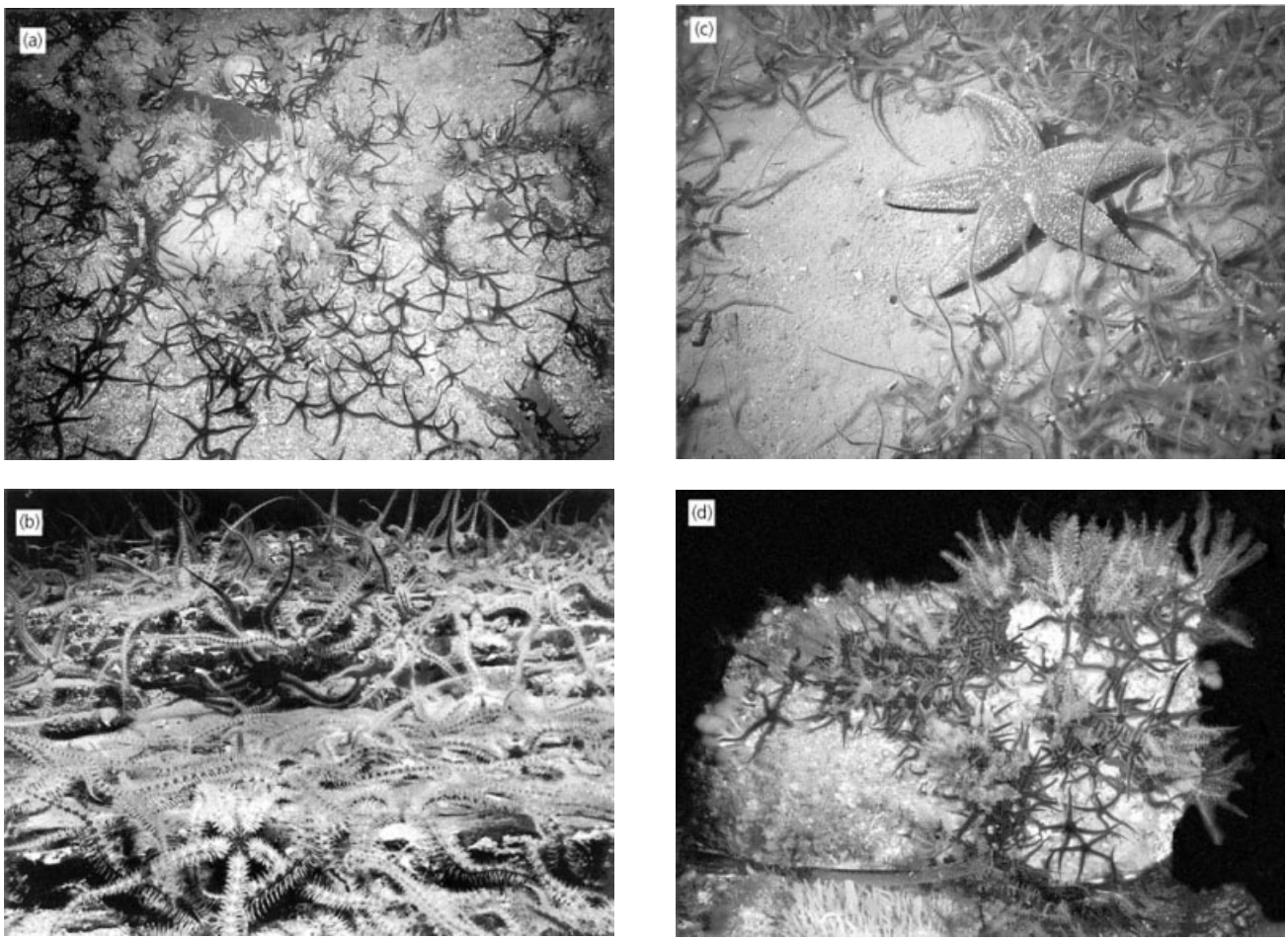

Fig. 4.1.7.1 Dense ophiuroid and crinoid populations in modern marine environments around the British Isles. All photographs are at 10 m depth. (a) *Ophiocomina nigra* off Torbay, English Channel; disc diameters ≈ 16 mm. (b) *Ophiothrix fragilis* suspension feeding off Torbay; disc diameters ≈ 13 mm. (c) *Ophiothrix fragilis* retreating from the sea star *Asterias rubens* in Loch Melfort, west coast of Scotland; the *Asterias* is moving from left to right, creating a 'bow wave' of fleeing *Ophiothrix*. (d) Aggregation of *Ophiocomina nigra* and the comatulid crinoid *Antedon bifida* off the Isle of Cumbrae, west coast of Scotland. (a,b,d, Courtesy of G.F. Warner.)

The ecological history of crinoids is similar to that of ophiuroids. Stalked crinoids were abundant in shallow water in the Palaeozoic and early Mesozoic, but they live only in deep water today. After durophagous predators eliminated stalked crinoids from shallow-water environments, the comatulid (unstalked) crinoids diversified in shallow water (Fig. 4.1.7.1d; Meyer and Macurda 1977). In general, from the Triassic onward epifaunal suspension feeders in level-bottom habitats were replaced by infaunal suspension feeders such as bivalves, and by more mobile epifaunal suspension feeders such as comatulids. Durophagous predation is an important reason why infaunal bivalves dominate nearshore assemblages in the Cenozoic.

Trends in time and space

Predator–prey relationships do not evolve in an ecological vacuum. Increased productivity in the Mesozoic probably supplied the energy required to drive the acquisition of antipredatory features. The Mesozoic innovations of predators and prey transcended the end-Cretaceous mass extinction and subsequent intervals of elevated extinction in the Cenozoic. Those extinctions temporarily set back morphological trends in prey, however, by selectively wiping out well-defended forms (Vermeij 1987).

Temporal trends in durophagy are mirrored by modern biogeographical patterns. Shell-breaking predation increases with decreasing latitude, and the defensive features of gastropod shells increase along the same

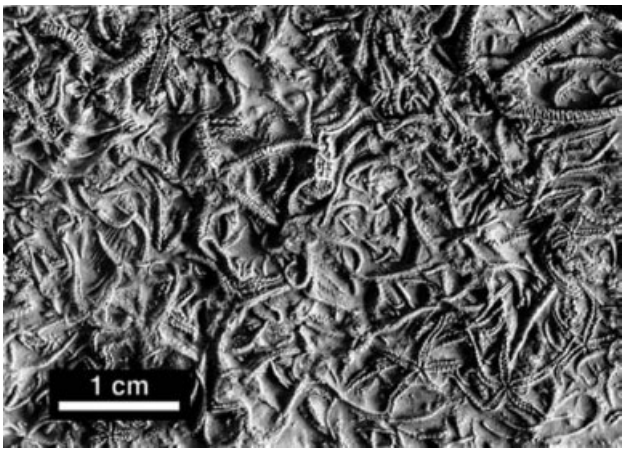

Fig. 4.1.7.2 Dense, autochthonous, shallow-water assemblage of the Early Mississippian ophiuroid *Strataster ohioensis* from North Royalton, Ohio. (From Kesling and Le Vasseur 1971, with permission.)

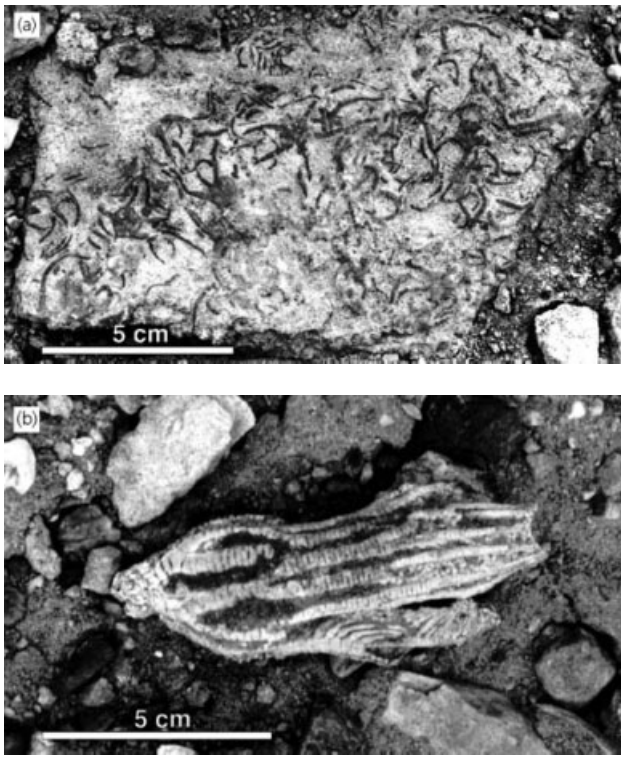

Fig. 4.1.7.3 Fossil ophiuroids and crinoids from the Late Eocene La Meseta Formation, Seymour Island, Antarctica. (a) Dense, autochthonous assemblage of *Ophiura hendleri*. (b) The stalked crinoid *Metacrinus fossilis*, which is also found in autochthonous aggregations.

latitudinal gradient. Predator–prey relationships have evolved to a greater extent in the tropics partly for physiological reasons: crushing activity and calcification are more rapid and less energetically expensive at higher temperatures. As a result, mollusc shells are thick and ornate in the tropics but thin and plain at high latitudes. Although low temperatures depress the activity of shell-drilling gastropods, drilling generally increases with increasing latitude, because the drillers themselves are less prone to predation.

Global climate change can affect predator–prey interactions in a manner predictable from latitudinal patterns, introducing a geographical component to temporal trends. Dense, autochthonous assemblages of ophiuroids and of stalked (isocrinid) crinoids occur in the Late Eocene La Meseta Formation at Seymour Island, Antarctic Peninsula (Fig. 4.1.7.3). Their common occurrence in a shallow-water setting in the Palaeogene is at variance with their supposed absence from shallow water after the Mesozoic. These echinoderm palaeopopulations display extremely low frequencies of sublethal arm damage, indicating low predation pressure. They are concentrated near the top of the La Meseta Formation, which represents the end of the Late Eocene. Global cooling at that time probably disrupted predator–prey relationships in Antarctica by changing the geographical and bathymetric distributions of both predators and prey. Decapods, for instance, essentially vanished from shallow water, and they never returned. The decreased intensity of durophagous predation at the end of the Late Eocene allowed anachronistic, Palaeozoic-type communities dominated by ophiuroids and crinoids to reappear (Aronson *et al*. 1997). Living benthic communities in shallow water in Antarctica are characterized by a depauperate fish fauna and no decapods; low levels of shell-crushing predation; high levels of predation by sea stars and drilling gastropods; and dense populations of epifaunal, suspension-feeding echinoderms.

The effects of global cooling on shell-breaking and shell-drilling predation of Eocene molluscs in Antarctica have not been investigated. Despite this and other deficiencies, enough information on the palaeontology, ecology, and biogeography of durophagous predation now exists to make predictions about the effects of global warming over the next decades to centuries. One prediction is that warmer temperatures and the resultant expansion of tropical and subtropical predators to higher latitudes will promote the phenotypic or genetic acquisition of more effective architectural defences in resident prey populations.

References

Aronson, R.B. (1994) Scale-independent biological interactions in the marine environment. *Oceanography and Marine Biology: an Annual Review* **32**, 435–460.

Aronson, R.B., Blake, D.B. and Oji, T. (1997) Retrograde community structure in the late Eocene of Antarctica. *Geology* **25**, 903–906.

Kelley, P.H. and Hansen, T.A. (1996) Naticid gastropod prey selectivity through time and the hypothesis of escalation. *Palaios* **11**, 437–445.

Kesling, R.V. and Le Vasseur, D. (1971) *Strataster ohioensis*, a new Early Mississippian brittle-star, and the paleoecology of its community. *Contributions from the Museum of Paleontology, University of Michigan* **23**, 305–341.

Meyer, D.L. and Macurda, D.B. Jr (1977) Adaptive radiation of the comatulid crinoids. *Paleobiology* **3**, 74–82.

Signor, P.W. and Brett, C.E. (1984) The mid-Paleozoic precusor to the Mesozoic marine revolution. *Paleobiology* **10**, 229–245.

Vermeij, G.J. (1987) *Evolution and escalation*. Princeton University Press, Princeton.

West, K., Cohen, A. and Baron, M. (1991) Morphology and behavior of crabs and gastropods from Lake Tanganyika, Africa: implications for lacustrine predator–prey coevolution. *Evolution* **45**, 589–607.

4.1.8 Buoyancy, Hydrodynamics, and Structure in Chambered Cephalopods

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Introduction

Only a few modern cephalopods have a chambered shell: the externally shelled *Nautilus*, and the internally shelled *Spirula* and sepiid cuttlefish. However, this belies a taxonomically and morphologically diverse fossil history. Chambered cephalopods sustain hydrostatic forces on the shell, and must bear the energetic costs of moving the bulky shell through the water. These structural and hydrodynamic constraints tend to conflict. Shell shapes that confer strength are often not hydrodynamically advantageous. This adaptive conflict in shelled cephalopods may help to explain the repeated evolution of similar suites of morphological features, including shell shape and sutural pattern.

Emptying the chambers

Successive addition of septa during growth partitions the cephalopod shell into chambers. Septa also occur in some gastropods, and occasionally in bivalves. However, the siphuncle, which empties the chambered shell, is unique to cephalopods (Fig. 4.1.8.1). The siphuncle appeared in the Cambrian as a tube penetrating the serial chambers of a molluscan shell (sepiids subsequently evolved a sheet-like siphuncle). The siphuncle contains one or more arteries that bring oxygen and nutrients to the metabolically active 'pumping' epithelium that lines the siphuncular tube. The tube consists of the extended 'necks' of the calcareous septa joined by a series of connecting rings composed of a connective tissue (conchiolin). These rings are strong, yet permeable to fluids. Epithelial cells pump out the chambers using a hyper-osmotic pump (Greenwald *et al.* 1982). A sodium-ion membrane transport system concentrates ions in tiny channels in the epithelial cells, drawing water into the channels through osmosis, and forcing it into the siphuncle against hydrostatic pressure. This mechanism allows chambered cephalopods to empty their shells at considerable depth in the sea.

As the shell empties, a vacuum forms in the chambers. Gas then diffuses into the chambers until an equilibrium is reached with the CO_2-enriched dissolved gases in the blood. At no time does the gas in the chamber exceed atmospheric pressure. Gas pressure plays no role in emptying the shell. A pressure difference exists between the inside and the outside of the shell proportional to the depth to which the cephalopod descends, resulting in stresses in the structure of the shell.

Diurnal migrations in cephalopods were long assumed to result from buoyancy change. However, daily buoyancy changes are only feasible in shallow water in forms with large ratios of siphuncle area to chamber volume (Ward 1982). Sepiids have a large siphuncular area and change density daily, remaining on the bottom during the day and feeding in the water column at night. Fossil endoceratids had large siphuncles and may have migrated in a diurnal density-dependent manner. In other cephalopods, the chambered shell serves to maintain neutral buoyancy and vertical migration requires active swimming.

Stability

In the Cambrian and Ordovician, straight and minimally coiled cephalopod shells were the norm. The buoyant shell 'floated' above the dense body resulting in a stable 'face-down' orientation limiting lateral movement. To compensate for this, many Palaeozoic groups deposited carbonate in the shell apex, either in the siphuncle (endoceratids, actinoceratids, discosorids, oncocerids, orthocerids) or in the chambers (some orthocerids and nautilids). This 'counterbalance' permitted horizontal orientation, and facilitated lateral movement. Palaeozoic ascoceratids reduced stability by breaking off the apex of the growing shell, and Mesozoic belemnites weighted the apex of their internal shell. From the Devonian onwards coiled shell forms predominate. Coiled shells resist predation and the transition to coiled forms is contemporaneous with the diversification of jawed verte-

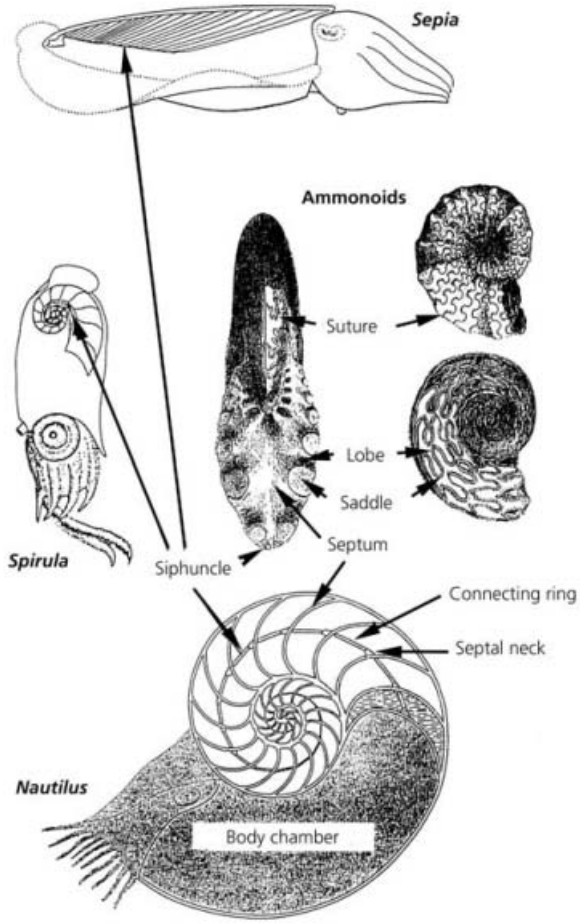

Fig. 4.1.8.1 Shell form and terminology in modern, and some fossil, chambered cephalopods. *Nautilus* and many fossil cephalopods had external shells (ectocochliate). Some modern cephalopods, such as *Sepia* (the cuttlefish) and *Spirula*, have internal chambered shells, and many others have reduced shells that lack chambers. Septa partition the shell into chambers, and the siphuncle pumps fluid out of the chambers so that the shell functions in buoyancy compensation. The siphuncle is usually a tubular structure that penetrates the chambers. However, in *Sepia* a sheet-like siphuncle forms one surface of the chambered shell. Where a septum meets the shell wall a suture line is formed. In many cases this line is not straight as it reflects waves in the septum. Convex folds of the suture and septum that point out into the body chamber (adoral) are referred to as *saddles*. Concave folds that open toward the body chamber and point into the shell (adapical) are referred to as *lobes*. Ammonoids are well known for the complex folding of their sutures. (After Jacobs 1992.)

brates. Coiled cephalopods may also be more effective swimmers.

In *Nautilus* stability plays a key role during jet-propelled swimming. The jet emanates from the funnel near the ventral shell margin. Consequently, the shell rotates as the pulse of the jet propels it forward. The dense body then swings back beneath the buoyant phragmocone. Application of a stability-based 'pendulum-like' swimming model, based on *Nautilus*, to ammonoids suggests that they were poor swimmers. However, Mesozoic ammonoids, which have longer body chambers than *Nautilus*, preferentially evolved reduced stability. The *Nautilus* model may not be relevant to these forms as the jet did not emanate from a ventral location; ammonoid swimming may have been more like that of the more closely related coleoids.

Nautilus directs the jet downward to excavate sediment in benthic feeding and back under the shell to swim forward. Shell stability and a siphonal notch are also characteristic of some late Palaeozoic ammonoids, suggesting a ventral jet and forward locomotion, or benthic excavation. More generally, lineages of straight and coiled cephalopods evolved reduced stability, facilitating dynamic control of orientation and locomotion.

Hydrodynamic issues

Neutral buoyancy permits cephalopods to swim without expending energy to overcome gravity. Muscular compression of the mantle cavity expels water out of the funnel; such jet propulsion is a major mode of swimming in living cephalopods. Coleoids also use fins to swim. However, the volume displaced by the chambered shell increases the costs of locomotion. So which shell shapes least impede swimming?

In coiled cephalopod shells, prominent ornament and a well-defined umbilicus increase drag. The degree of lateral compression required to minimize drag depends on size and swimming speed (i.e. on Reynolds number). Highly compressed shells experience less drag at large size and velocity; thicker forms incur less drag at small size and velocity (Fig. 4.1.8.2). This results from a trade-off between 'skin friction' and 'pressure' drag. Larger animals can swim faster; pressure drag predominates, and thinner forms often have an advantage due to a smaller cross-sectional area. Small cephalopods experience lower drag if they are thicker, as reduced surface area minimizes skin-friction drag at lower Reynolds numbers. Changes in shape with increasing size during ontogeny, and responses in shell shape to differences in environmental flow regime, result from this trade-off (see Jacobs and Chamberlain 1996 and references therein).

Acceleration imparts costs associated with the acceleration of the mass of the organism and the acceleration of the mass of water in its wake (added mass). If the acceleration is frequent, as it may be in jet propulsion, added mass will be a substantial fraction of the cost of locomotion. Frequent evolution of narrow, tapered 'oxyconic' shells may reflect adaptation for acceleration, as oxycones appear to be overdesigned for drag reduction alone. Orthocones may also have been efficient in

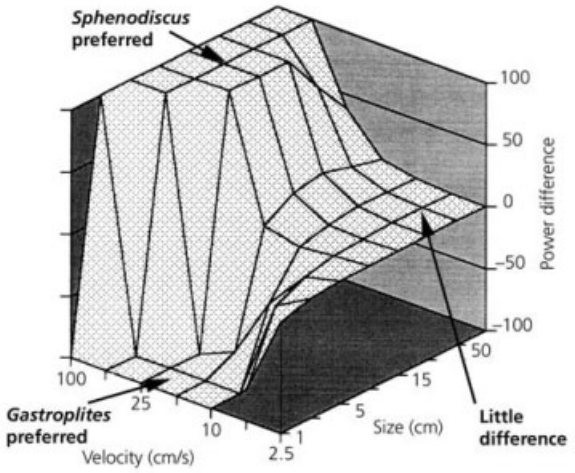

Fig. 4.1.8.2 Differences in power required per unit volume as a function of size and swimming velocity, in a laterally compressed form, *Sphenodiscus*, and a form of intermediate thickness, *Gastroplites*. The surface is based on interpretation of drag force data, and was generated by subtracting power required per unit volume [(ergs/s)/cm^3] in *Sphenodiscus* from similar values pertaining to the same size and velocity in *Gastroplites*. When values are negative, such as at small sizes and modest velocities, the thicker *Gastroplites* form requires less power per unit volume. At large size and high velocity the thin *Sphenodiscus* form has lower power loss due to drag. (After Jacobs and Chamberlain 1996.)

acceleration, perhaps permitting a lunging predatory mode of life.

Living *Nautilus* and *Vamproteuthis* have the lowest metabolic rates found in swimming organisms. Pelagic squid, such as *Illex*, muster huge amounts of energy to support their costly jet-propelled lifestyle. Thus a range of activity can be envisioned for fossil cephalopods. In fast swimmers the costs of transporting a bulky shell exceeds the advantages of neutral buoyancy and protection. In coleoid evolution, chambered shells are first internalized to minimize their hydrodynamic costs, and then completely lost in lineages that evolved the most active swimming. Loss of the chambered shell also occurs in cephalopods with a benthic mode of life (e.g. *Octopus*, and some sepiids such as *Rossia*).

Structural issues

Removal of fluid from the chambered cephalopod shell permits neutral buoyancy. It also results in a pressure difference across the shell generating a structural problem. The shell must resist implosion, and the strength of the shell limits the operational depth. Realization of this relationship led to calculations of the depth limits of modern and fossil cephalopods based on the failure strength of various shell components. Stresses in pressure-loaded spheres and tubes are readily calculated. Consequently, the tubular siphuncle provides a means of relating strength of material to habitat depth. Estimates of depth limits based on such calculations generally agree with depth assessments based on sedimentological criteria.

Cephalopod shells, composed of layers of nacreous and prismatic carbonate materials, are toughened by their microstructure and organic matrix. Nevertheless, these are brittle materials, substantially stronger in compression than in tension. Consequently, a chambered shell will be able to generate more buoyancy, with less carbonate material and hydrodynamic cost, if tensile stresses are minimized.

Spheres and tubes exposed to external hydrostatic load generate compressive stresses. If structural support of hydrostatic load was the only selective force operating, then shell shapes that were nearly circular in cross-section (either globose coiled forms or orthocones) would be anticipated. Orthocones with a relatively circular whorl section predominated in the early Palaeozoic. The shell wall of these forms experienced compression. The septa are concave with simple sutures. Only the siphuncle and last-formed septum experienced tension. The open coil and circular whorl section of the modern *Spirula* shell supports pressure equivalent to 1600 m of water, showing that such simple shells are well suited to resist hydrostatic load (see Jacobs 1992 for discussion).

Sutures and shell shape

Departure from a circular whorl section results in stresses that can no longer be borne around the shell purely in compression. The resultant bending produces non-adaptive tensile stress in the brittle shell material. Competing adaptive influences, such as hydrodynamic factors, may be required to explain such evolution. Features that minimize bending stresses would be expected in forms that depart from a circular whorl section. Septal supports that reduce span lengths in the flattest portions of the shell wall are one such feature. Relative to putative ancestors such as the globose *Eutrephoceras*, *Nautilus pompilius* evolved lateral compression and a single lobe in the suture. Although concave dorsoventrally, the lobe in the *Nautilus* suture forms a flat strut in the lateral traverse of the septum between the flanks. The shell wall flexes over this strut during hydrostatic loading, documenting septal support of the shell wall (Hewitt and Westermann 1987). Evolution of laterally compressed shells with extensive flat flank regions coincides with the introduction of dramatic lobes and saddles in the sutures of other Cretaceous/Tertiary (e.g. *Aturia* and *Hercoglossa*) and Late Triassic (e.g. *Siberionautilus* and *Gonionautilus*) nautiloid lineages (see Westermann 1975). Thus in multiple nautiloid lineages sutures coevolve

with shell shape in a manner consistent with the support of the shell wall by the septum.

Ammonoids

In Mesozoic ammonoid lineages, the evolution of laterally compressed shells coincides with the introduction of sutural elements supporting the flattened flanks. This is comparable to, but much more extensive than, the introduction of sutural elements and septal support seen in nautiloid lineages. Complex frilling in some ammonoid sutures may be accessory to struts supporting the shell. A rigid septum meeting the shell wall at a right angle generates bending stresses in the shell wall as the shell passes over the support (Hewitt and Westermann 1987). The thin septa of many Mesozoic ammonoids meet the shell wall at an angle in a series of folds. This thin frilled margin may permit limited elastic response in the septum, diffusing septal support over an area of the shell wall.

Despite the complex frilling of the sutures in many ammonoids, the overall sutural pattern still responds to shell shape. In laterally compressed shells, with variable curvature around the whorl, the size of spaces between sutural support is largest in the tightly curved ventral region and smallest in the flatter flank regions (Fig. 4.1.8.3). In globose ammonites, with uniform curvature of the shell surface, the span sizes (spaces between regions of the shell supported by sutures) are roughly equal around the shell (Jacobs 1990).

Different loading of the last septum

Cephalopod shells are loaded in two different ways during ontogeny. The phragmocone (chambered portion of the shell) is subject to pressures operating on the external surface of the shell wall. However, in the case of the last-formed septum, pressure also acts through the body, loading the adoral surface of this septum. Furthermore, load transferred to this septum from the shell wall will be asymmetric, with the adapically pointing lobes supporting a greater load than the saddles that point into the body chamber. This asymmetry of load may explain why lobes are more elaborately frilled than saddles in many ammonoids (Fig. 4.1.8.1). In addition, the last septum secreted during ontogeny forms the back of the body chamber in the adult. This septum bears the load from the body chamber through adult life. In many cases this septum is thicker than, or in close proximity to, the preceding septum, suggesting that load through the body chamber is a factor influencing septal morphology.

Conclusion

Sutural complexity is associated with the evolution of shell shapes with non-circular whorl sections. In some cases sutural evolution is associated with dorsoventrally depressed or quadrate whorl shapes. However, correlated evolution of suture and whorl shape is best documented in lineages that have become laterally compressed. Lateral compression has hydrodynamic implications. Given the relationship of hydrodynamic features to shell shape, and the relationship of shell shape to whorl section and sutural pattern, it is not surprising to find cases of iterative evolution of similar form in different ammonoid lineages. This homeomorphy may occur in response to similar changes in environment, such as the shallowing of basinal settings. Further progress in understanding the functional evolution of cephalopods in general, and the evolution of homeomorphs in particular, may be possible through detailed examination of morphological change in sutures and shell shape in concert with detailed studies of changing sedimentary environments in stratigraphic sections.

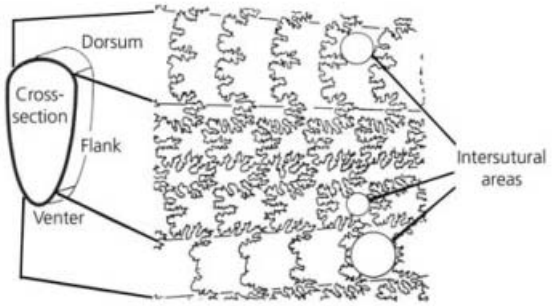

Fig. 4.1.8.3 Shell curvature and sutural pattern in *Baculites compressus*. Note the inverse relationship between the unsupported span size, the circles, and the curvature of the shell. This relationship minimizes tensile stresses due to bending in a shell with variable surface curvature. (After Jacobs 1990.)

References

Greenwald, K.P., Cook, C.B. and Ward, P. (1982) The structure of the chambered *Nautilus* siphuncle: the siphuncular epithelium. *Journal of Morphology* **172**, 5–22.

Hewitt, R.A. and Westermann, G.E.G. (1987) *Nautilus* shell architecture. In: W.B. Saunders and N.H. Landman, eds. *Nautilus*, pp. 435–461. Plenum, New York.

Jacobs, D.K. (1990) Sutural pattern and shell stress in *Baculites* with implications for other cephalopod shell morphologies. *Paleobiology* **16**, 336–348.

Jacobs, D.K. (1992) The support of hydrostatic load in cephalopod shells: a history of adaptive and ontogenetic explanations in morphology and evolution. *Evolutionary Biology* **26**, 287–349.

Jacobs, D.K. and Chamberlain, J.A. Jr (1996) Hydrostatic and hydrodynamic issues in ammonoid functional morphology.

In: N.H. Landman, K. Tanabe and R. Davis, eds. *Ammonoid paleobiology*, pp. 169–224. Plenum, New York.
Ward, P.D. (1982) The relationship of siphuncle size to emptying rates in chambered cephalopods: implications for cephalopod paleobiology. *Paleobiology* **8**, 426–433.
Westermann, G.E.G. (1975) A model for origin, function and fabrication of fluted cephalopod septa. *Paläontologische Zeitschrift* **49**, 235–253.

4.1.9 Feeding in Conodonts and other Early Vertebrates

M.A. PURNELL

Introduction

Hypotheses of feeding are intimately bound up with scientific accounts of the early evolutionary history of vertebrates. The origin of vertebrates (= craniates), for example, has been linked to an ecological shift from suspension feeding to active predation, and changes in feeding mechanism are also invoked in various scenarios that seek to explain the origin of gnathostomes (vertebrates with jaws) from among the agnathans (jawless vertebrates) (see references in Purnell 1995; Pough *et al.* 1996). Competition for food resources has also been invoked to explain the decline of agnathans and the rise of jawed vertebrates (see Pough *et al.* 1996). Feeding in early vertebrates, however, is not well understood.

The Agnatha is a paraphyletic grouping of jawless fish (see Section 1.3.2), including anaspids, arandaspids, astraspids, conodonts, galeaspids, hagfish, heterostracans, lampreys, osteostracans, pituriaspids, and thelodonts (see Janvier 1996); the armoured members of this group are often referred to as ostracoderms. Except for lampreys and hagfish, all agnathans are extinct, and direct observation of feeding is not possible. The functional analysis of organisms known only as fossils must be based on comparisons with living organisms, and in many cases these comparisons ultimately depend on an hypothesis of homology at some level. But where relationships and homology are unknown or poorly constrained, hypotheses of function may rest entirely on analogy. Unfortunately, functional hypotheses based on analogy are difficult to test and may be little more than speculation. This has hampered the understanding of feeding in extinct agnathans: they were jawless, but possessed a variety of oropharyngeal feeding structures (e.g. the phosphatic elements of the conodont apparatus, the oral plates of heterostracans and osteostracans, and the mandibular plate of anaspids) which lack homologues in extant taxa. Consequently, hypotheses of feeding have ranged widely, with little evidence of a consensus emerging.

Feeding in conodonts

Until quite recently, feeding in conodonts was probably less well understood than in any other group of fossil agnathans. Now that the agnathan affinities of conodonts are known (see Section 1.2.4), however, analysis of the function of their phosphatic elements and their feeding mechanisms has taken on new significance for understanding the early evolution of vertebrates. From the evidence of the few specimens that preserve remains of conodont soft tissues, it is clear that the elements were located in the oropharyngeal region of the head. Natural assemblages preserving elements in their original, but flattened, arrangement indicate that they formed a bilaterally symmetrical array. There is no longer any dispute that this apparatus was involved in feeding, but what is more contentious is whether it formed a suspension-feeding structure, or functioned as a set of teeth. Both these hypotheses are supported by analogies with living organisms, but the elements lack homologues among extant taxa. Nor was the debate regarding function resolved by the discovery of soft-tissue remains of conodonts (see Purnell 1999). However, testable predictions of apparatus growth rates can be derived from hypotheses of function. If the conodont apparatus formed a filtering device, the food intake of the animal would have been dependent on the surface area of the filtering array formed by the anterior elements of the apparatus, and in an isometrically growing animal this would have increased in proportion to body mass to the power 0.67. Food requirements, however, are linked to metabolic rate, which increases in proportion to body mass to the power 0.75. Thus, the increasing metabolic demands of a growing conodont would require positive allometry of the elements involved in filtering. No taxa for which apparatus growth rates have been analysed quantitatively exhibit positive allometric growth (see Purnell 1999). This indicates that conodonts were not suspension feeders.

This test may be quantitative, but it is none the less inferential, and relies on certain assumptions regarding conodont growth (Purnell 1999). However, direct evidence of feeding in conodonts has been obtained from the analysis of wear and surface damage on conodont elements. Damage to feeding structures produced during their normal use provides a fundamentally different type of evidence to that obtained from functional analysis of morphology. For fossils such non-structural evidence represents the closest approximation to direct

observation of function (Purnell 1999). Of particular significance in conodonts is the development of microwear textures within wear facets on functional surfaces (Fig. 4.1.9.1). These are comparable to the microwear textures developed on the teeth of mammals, and allow precise characterization of feeding in conodonts. The smooth, polished areas on the blade of *Gnathodus bilineatus* (Fig. 4.1.9.1a), for example, indicate either that this part of the element was in contact with the opposed blade without intervening food, or more likely that the species ate food that was not abrasive. The pitted microwear on *Idiognathodus* platforms (Fig. 4.1.9.1b) indicates that food was crushed between opposed elements, but the lack of associated scratches indicates that they did not grind. The parallel scratching on elements of *Ozarkodina confluens* (Fig. 4.1.9.1c) and *Drepanoistodus* (Fig. 4.1.9.1d) is diagnostic of shearing. The scratching reflects the abrasiveness of the food consumed, and it is probable that *Drepanoistodus* ate food that contained more abrasive particles than the food of *O. confluens*. Also, the degree of parallelism of scratches on teeth reflects the tightness of occlusal guidance, and given that conodonts were jawless, suggests surprisingly precise control of element motion and contact. This

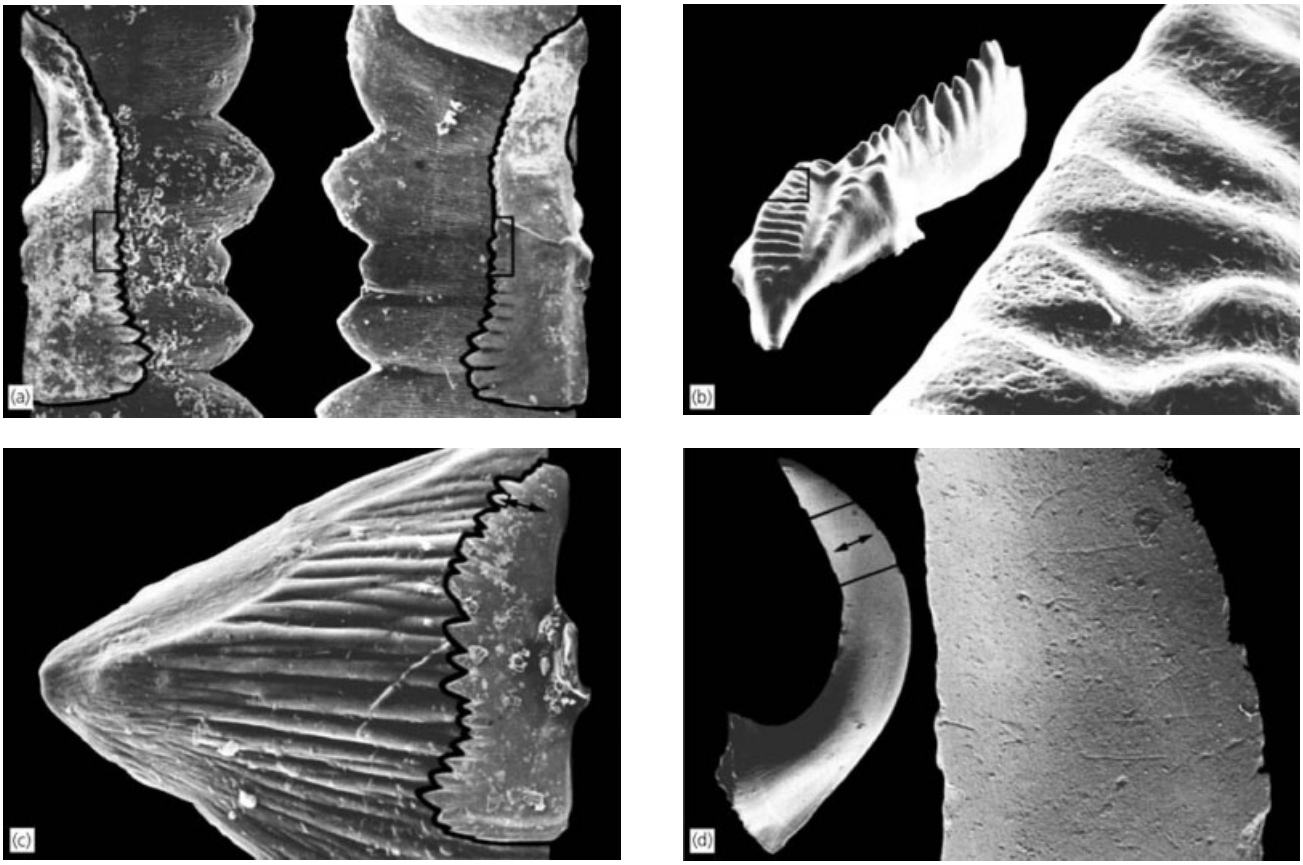

Fig. 4.1.9.1 Microwear in conodont elements. (a) Pa element of *Gnathodus bilineatus* (Carboniferous, UK); the original fibrous surface texture is well preserved on the anterior surface of the element (shown on left) but has been worn off the posterior surface (shown on right) where it was in contact with the opposed element; this wear, on one side only, cannot be the result of postmortem abrasion; whole element ×26, close-up ×208. (b) Pa element of *Idiognathodus* (Carboniferous, USA); the crests of the platform ridges in this element are blunted and flattened to form triangular wear facets with pitted microfeatures; such features are not developed elsewhere on the element and are most unlikely to be postmortem artefacts; whole element ≈ ×33, close-up ≈ ×350. (c) Pa element of *Ozarkodina confluens* (Silurian, UK); a well-developed wear facet formed by contact with the opposed element sharply truncates the original fibrous surface texture; the facet is covered with fine, parallel striations (arrows indicate orientation of shearing motion); the distinctive nature of this facet and its location, between denticles, preclude a postmortem origin; whole element ×35, close-up ×1227. (d) Element of *Drepanoistodus* (Ordovician, Saudi Arabia), apex tilted a little towards viewer; a number of straight, parallel scratches traverse the slightly convex surface; their parallelism precludes a postmortem origin (arrows indicate orientation of shearing motion); whole element ≈ ×33, close-up ≈ ×174. (After Purnell 1995; © Macmillan Magazines Ltd.)

applies even to *Drepanoistodus*, which bore only simple cone-shaped elements and belongs to a primitive order of the Conodonta dating back to the Late Cambrian. The broader significance of shearing for hypotheses of feeding lies in the fact that it represents a method of food breakdown that is incompatible with microphagy, thus providing unequivocal evidence that conodonts were macrophagous.

Food processing in conodonts can now be analysed in detail based on wear and surface damage, but hypotheses of food acquisition are, as yet, unsupported by such direct evidence. The skeletal architecture of ozarkodinid conodonts, however, provides some new physical constraints derived from the spatial arrangement of the elements (Purnell and Donoghue 1997). This work suggests that the comb-like S and M elements at the anterior of the apparatus were attached to a pair of cartilaginous dental plates, similar to those of extant agnathans, and that when in use these plates were pulled forwards and pivoted over the anterior edge of an underlying ventral cartilage. The resulting anterior and ventral motions opened the apparatus; grasping was brought about by the reverse action, producing a net posterior and inward rotation of the elements, as indicated by the arrows on Fig. 4.1.9.2. This motion need not have been a steady, smooth action; as the dental plates pivoted over the anterior edge of the underlying cartilage the apparatus may have snapped back into the closed position, in a manner similar to closure of the hagfish lingual apparatus. This hypothesis of grasping was based on a detailed architectural model of the ozarkodinid apparatus, but it is probably also applicable to other groups of conodonts with comparable spatially differentiated apparatuses, such as prioniodinids and prioniodontids. These groups represent fairly derived conodonts, however, and although food acquisition in primitive coniform taxa may have involved a similar mechanism of closure, the details are currently unknown.

Hypotheses of feeding in other early vertebrates

Although a bilaterally operating feeding apparatus is a synapomorphy of vertebrates (Purnell and Donoghue 1997), there is no evidence that any other extinct agnathans possessed an eversible feeding apparatus. Similarly, there is no evidence to support the hypothesis that the conodont apparatus is directly comparable to the oral or pharyngeal structures of ostracoderms. In fact, these structures have not been subjected to rigorous functional analysis and, apart from the conodonts, hypotheses of feeding in extinct agnathans are poorly constrained and generally speculative. Evidence from the few specimens that preserve gut contents is inconclusive, and some hypotheses are based on nothing more than gross body shape and inferred mode of life (see Janvier 1996). Many mutually exclusive alternatives have been proposed, and hypotheses of feeding in heterostracans and anaspids, just two groups of agnathans, provide a good illustration of the problem. Published interpretations include predation (with or without rasping tongue), mud grabbing, microphagous suspension feeding, deposit feeding, algal frond snipping or scraping, plankton feeding, detritivory, and suction

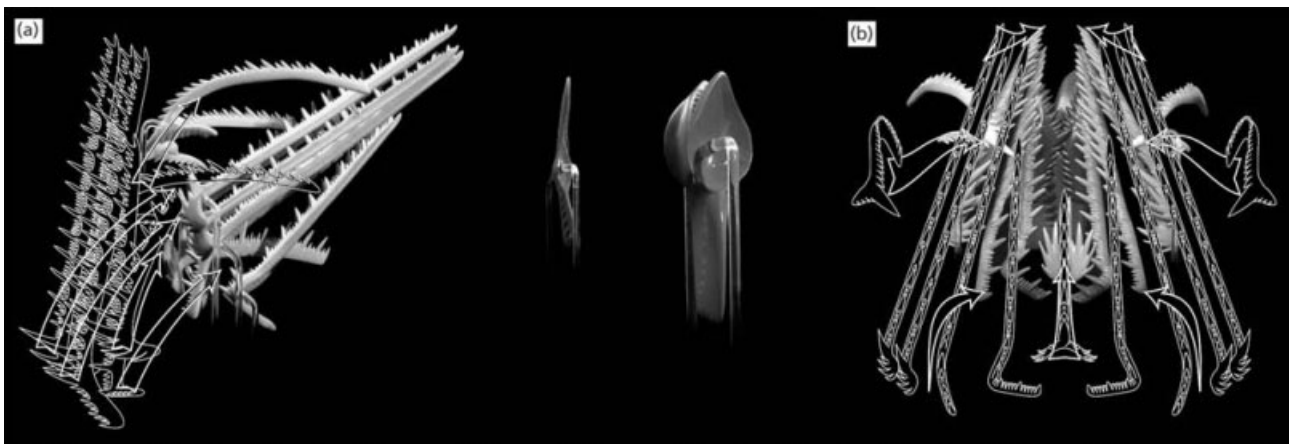

Fig. 4.1.9.2 Hypothesis of grasping by anterior elements of ozarkodinid apparatus. Elements drawn in outline indicate their position when the apparatus is everted and open; photographs show elements in the retracted position. (a) Lateral view of apparatus; arrows indicate net movement of the S and M elements during retraction and closure of the anterior array. (b) Anterior view of apparatus; arrows indicate net movement of S and M elements. (After Purnell 1999; modified from Purnell and Donoghue 1997.)

feeding. Some of these hypotheses are contradicted by what is known of the biology of agnathans; suction feeding, for example, is difficult to reconcile with evidence that without jaws agnathans were unable to generate strong suction (Purnell and Donoghue 1997). Other modes of feeding are at least possible but have yet to be tested thoroughly.

So, what are the implications for scenarios of early vertebrate evolution? The evidence that conodont elements functioned as the teeth of a primitive macrophagous vertebrate supports hypotheses that the first vertebrates were predators. Without more rigorous analysis of feeding in other extinct agnathans, however, hypotheses which link the evolutionary history of the early jawless vertebrates to changes in feeding mechanism or to competition from gnathostomes must be viewed as speculative.

References

Janvier, P. (1996) *Early vertebrates*. Oxford Monographs on Geology and Geophysics, No. 33. Clarendon Press, Oxford.

Pough, F.H., Heiser, J.B. and McFarland, W.N. (1996) *Vertebrate life*. Prentice Hall International, New Jersey.

Purnell, M.A. (1995) Microwear on conodont elements and macrophagy in the first vertebrates. *Nature* **374**, 798–800.

Purnell, M.A. (1999) Conodonts: functional analysis of disarticulated skeletal structures. In: E. Savazzi, ed. *Functional morphology of the invertebrate skeleton*, pp. 129–146. John Wiley, Chichester.

Purnell, M.A. and Donoghue, P.C.J. (1997) Architecture and functional morphology of the skeletal apparatus of ozarkodinid conodonts. *Philosophical Transactions of the Royal Society of London B* **352**, 1545–1564.

4.1.10 Locomotion in Mesozoic Marine Reptiles

M.A. TAYLOR

Introduction

The Mesozoic marine reptiles were the dominant predators of the seas (alongside some sharks) for almost 200 million years. They profoundly transformed the body form of land reptiles to meet the demands of marine life, and in so doing became classics of biological adaptation, recognized since the 1820s (Taylor *in* Callaway and Nicholls 1997). The most important groups included two groups of seagoing crocodilians, mosasaurs (Fig. 4.1.10.1a), ichthyosaurs (Figs 4.1.10.1b and 4.1.10.2), plesiosaurs with four wing-like limbs for underwater 'flight' (Figs 4.1.10.1c and 4.1.10.3), and placodonts (Fig. 4.1.10.1d), slow, sometimes armoured mollusc-eaters. Some grew huge: the largest plesiosaurs were around 15 m long, comparable to modern killer whales and sperm whales.

Swimming with body and tail

A lizard shows how the original reptilian body plan is inherently amphibious, even in land animals. When it runs, lateral undulations of the body and tail boost the movements of the legs. These undulations derive from axial swimming movements of ancestral amphibians and ultimately fish. They remain useful in water, the waves passing along the body and tail to provide a forwards thrust. Lizards and crocodilians swim in this way, as doubtless did the ancestors of most marine reptiles. Mosasaurs, early ichthyosaurs, and some marine crocodilians still swam like this, although their limbs were reduced and toes webbed or even fused into mitten-like fins. This body plan, producing thrust over most of the tail and even body, is suited to a burst of sudden acceleration. It especially suits ambush predators such as the modern Nile crocodile.

Animals which swim fast, or cruise for long distances, most efficiently produce thrust with a specialized hydrofoil surface. Moved transversely to the direction of motion, this hydrofoil produces a forwards lift force and so thrust. An example is the tail fin of many ichthyosaurs and whales, an oscillating analogue of the rotating screw propeller of modern ships. This was mostly stiff connective tissue, as can be seen in some exceptional ichthyosaur fossils, where the body outline is preserved as a black film (Fig. 4.1.10.2).

Jurassic ichthyosaurs were the most highly modified marine reptiles. The weight of their terrestrial ancestor—a vertical load—was borne by the vertebral column acting as a bridge or beam trestled between the fore and hind limbs. In the ichthyosaur, instead, the body was effectively supported by water, freeing the vertebral column to resist solely longitudinal loads. As the muscles on one side of the body and tail contracted against the flexible vertebral column, they swung the tail fin round to one side, generating a thrust force. The muscles on the other side then contracted in turn, swinging the tail back to the other side and providing further thrust. The spool-like, squatly cylindrical vertebrae were well suited to sustaining the resultant longitudinal compressive forces.

Streamlining

An animal moving through water encounters much

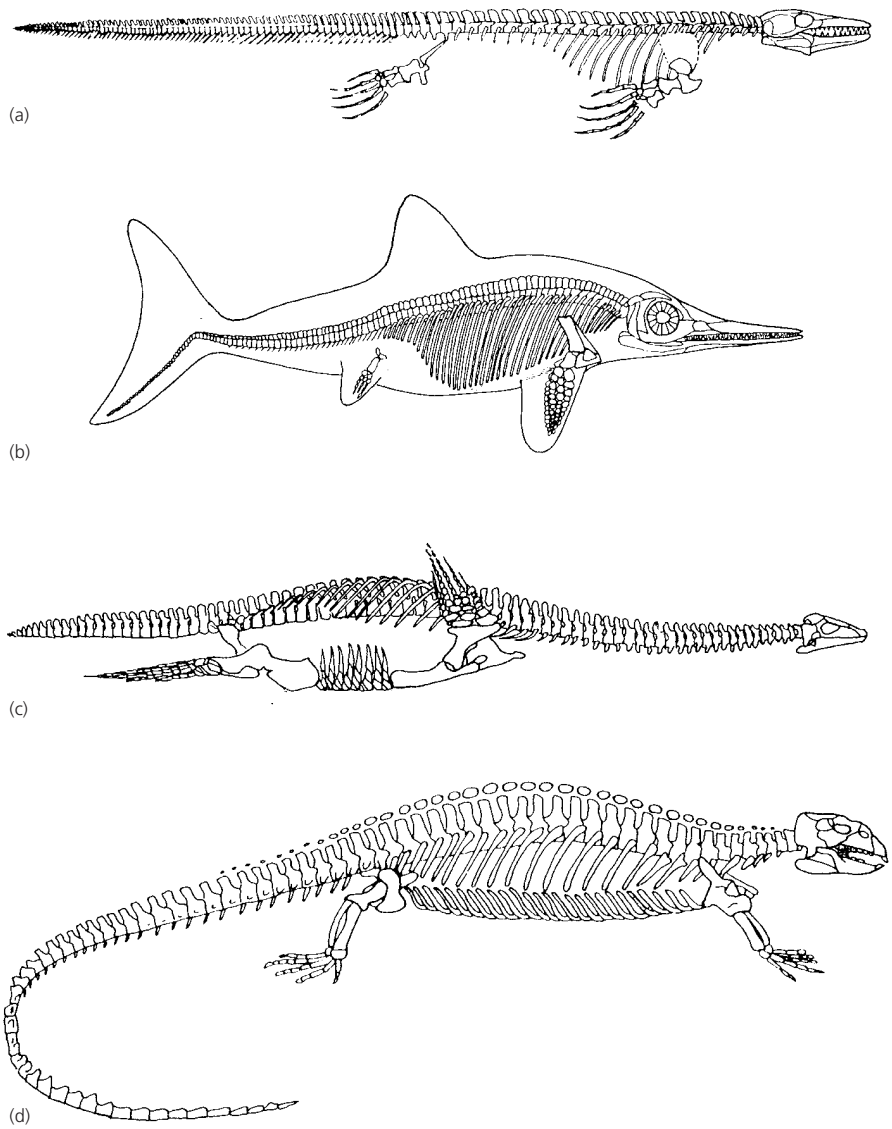

Fig. 4.1.10.1 (a) Late Cretaceous mosasaur *Platecarpus* (4 m). (b) Early Jurassic ichthyosaur *Ichthyosaurus* (1.4 m); skeleton with body outline based on the evidence of exceptionally well-preserved specimens (see Fig. 4.1.10.2). (c) Middle Jurassic plesiosaur *Cryptoclidus* (3 m). (d) Triassic placodont *Placodus* (1.5 m). (From Benton 2000, with permission.)

greater resistance ('drag') than in air, because water is far denser and more viscous. To minimize energy consumption and maximize speed, marine reptiles reduced drag, as far as is known, by streamlining (as in fishes and marine mammals): a typical trout-like teardrop body, rounded in cross-section, with a blunt front and tapering rear end, the smoothly blended surface minimizing turbulence and easing the flow of water over the body. At least some of this outline was the result of fat and connective tissue not normally preserved in fossils.

Directional control

It is not sufficient to swim forwards. It is also vital to control direction. In at least some ichthyosaurs, as in fishes and many whales, a dorsal fin passively stabilized the animal against rolling around its own longitudinal axis. However, most control was active. The limbs of ichthyosaurs were profoundly modified into unitary fins which acted as steering hydroplanes. These limbs no longer produced thrust, except perhaps minor swimming movements at low speeds. The shoulder and hip girdles bore neither the main locomotor muscles, nor the animal's weight, and became reduced. The hip girdle even lost the connection with the vertebral column necessary for support on land. Doubtless ichthyosaurs also controlled direction by altering the operation of the tail beat so as to change its angle of thrust.

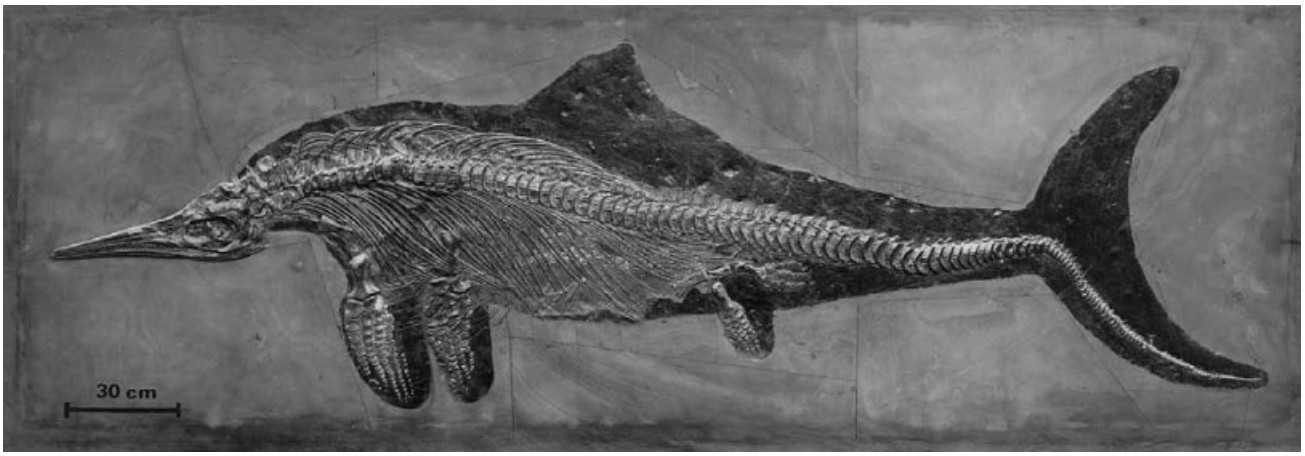

Fig. 4.1.10.2 An exceptionally well-preserved ichthyosaur skeleton (*Stenopterygius macrophasma*) from the Lower Jurassic Posidonienschiefer Lagerstätte at Holzmaden, south-west Germany, showing the body outline preserved as an organic film, including the dorsal fin and both lobes of the tail fin.

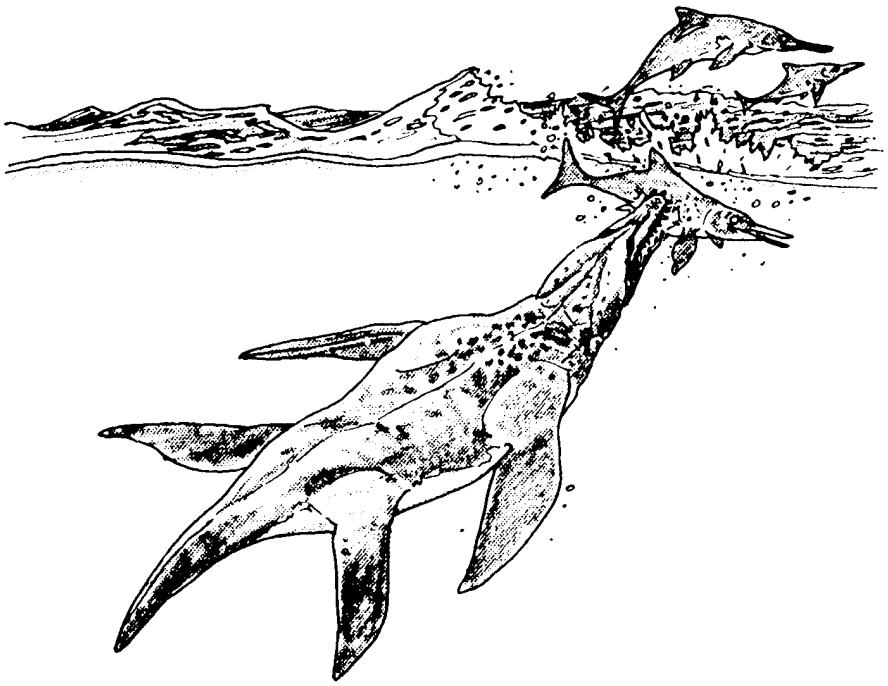

Fig. 4.1.10.3 A plesiosaur in life: *Liopleurodon*, ≈ 11 m long, attacking ichthyosaurs. (Courtesy of J.G. Martin/Leicester City Museum.)

The alternative solution: underwater 'flight'

Plesiosaurs swam not with their tails but with forceful beats of their wing-like limbs (Figs 4.1.10.1c and 4.1.10.3). Each limb became a single wing-like hydrofoil, operated by large muscles originating on the large bony plates of the shoulder and hip girdles. Plesiosaurs probably 'flew' through the water by flapping their limbs so that they provided forward-directed lift during part of the cycle, and pushed water backwards in a rowing action during another part of the cycle. Plesiosaurs apparently lacked specialized steering fins, and presumably steered by changing the lines of thrust produced by the limbs, although their head and sometimes enormously long neck could help steer the animal into a turn much as in sea-lions today. Modern analogues of plesiosaurs (sea-lions, penguins, and auks) also 'fly' underwater.

Buoyancy control

When an animal dives, its buoyancy depends on its density relative to that of water. Bone is around twice as dense as water, muscle a little denser than water, fat a little lighter, and air in the lungs much lighter. These tend to cancel out, so that marine reptiles were probably a little lighter than water because of the air in their lungs. The resulting tendency to rise had to be counteracted to allow the animal to stay at one depth (Taylor *in* Maddock *et al*. 1994; Taylor 2000). Fast swimmers simply swim a little more downwards to compensate ('hydrodynamic control'), as in whales and apparently in ichthyosaurs. Slower swimmers tend to increase the density of the body instead ('hydrostatic control'), by swallowing stones (e.g. penguins, sea-lions, crocodilians, and some plesiosaurs), or by adding bone to the skeleton (e.g. placodonts, manatees, and dugongs).

Coordination of locomotion with other adaptations

A key adaptation such as locomotion cannot be viewed in isolation; for example, feeding methods coordinate with locomotor adaptations (Massare *in* Maddock *et al*. 1994; Massare *in* Webb and de Buffrénil 1990; Callaway and Nicholls 1997). Marine reptiles presumably evolved largely to exploit aquatic food resources. But increasing adaptation to movement in water means reduced adaptation to movement on land. As a result, aquatic forms cannot move quickly or economically on land, if indeed at all; they catch live food less easily, and become more vulnerable to land carnivores. Placodonts (slow-swimming reptiles with heavy skeletons) retained limbs and feet, perhaps for basking on shore, but also probably to grip the sea bottom while they fed on hard-shelled invertebrates. They did not need to swim fast to catch such prey, any more than their modern analogue the sea otter *Enhydra*, or the herbivorous manatees and dugongs. By contrast, the high speed of ichthyosaurs allowed them to pursue active prey, such as fishes and cephalopods, using long snapping snouts to catch their victims.

Reproduction was probably the last tie to land, as in almost all modern marine mammals, birds, and reptiles. Like these, many Mesozoic marine reptiles probably came to land to lay eggs or give birth in isolated places free of land predators. In contrast, whales are fully aquatic and cannot move on land. Instead, the mother gives birth in water to live young, which emerges tail first so that it can swim rapidly to the surface for its first breath. Ichthyosaurs were no less ill-adapted for land movement, and fossils of gravid females have been discovered with embryos still in their ribcages (Fig. 4.1.10.2), indicating that ichthyosaurs also gave birth to live young (Benton 2000). Plesiosaurs, with a different body form, might have been able to move on land, to lay eggs or give live birth; or perhaps they gave live birth in the sea. No gravid females are known, but this is unreliable negative evidence as the lack of fossil gravid whales shows.

Convergence and its limits

The solutions evolved by the marine reptiles to the problems of life in water, over and over again, were repeated by their successors and ecological analogues, the marine mammals and birds, in a notable case of convergent evolution (Carroll *in* Callaway and Nicholls 1997). Thus plesiosaurs, sea-lions, and penguins adopted underwater flight; placodonts, sirenians, and sea otters developed bone ballast to feed on stationary food in shallow water; and ichthyosaurs and whales readopted a fish-like body form (Taylor *in* Maddock *et al*. 1994). However, differences in the ancestral forms mean that the results are not identical. For instance, when running, mammals tend to flex the body vertically rather than side to side as reptiles do. This difference accounts for the fact that whales swim by beating horizontal tail fins up and down, but ichthyosaurs swam by beating vertical tail fins from side to side. Convergence thus has its limits, even amongst marine vertebrates.

References

Benton, M.J. (2000) *Vertebrate palaeontology*, 2nd edn. Blackwell Science Ltd, Oxford.

Callaway, J.M. and Nicholls, E.L., eds. (1997) *Ancient marine reptiles*. Academic Press, San Diego.

Maddock, L., Bone, Q. and Rayner, J.M.V., eds. (1994) *Mechanics and physiology of animal swimming*. Cambridge University Press, Cambridge.

Taylor, M.A. (2000) Functional significance of bone ballast in the evolution of buoyancy control strategies by aquatic tetrapods. *Historical Biology* **14**, 15–31.

Webb, P.W. and de Buffrénil, V. (1990) Locomotion in the biology of large aquatic vertebrates. *Transactions of the American Fisheries Society* **119**, 629–641.

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4.1.11 Trackways—Dinosaur Locomotion

M.G. LOCKLEY

Introduction

It has been suggested that dinosaur trackways are the nearest thing to motion pictures of these extinct denizens of the Mesozoic. Despite a history of study dating back to the 1830s (Hitchcock 1858), research into fossil footprints (vertebrate ichnology) has only flourished as a subdiscipline since the 1970s, thanks in part to the so-called Dinosaur Renaissance which took a 'new look' at dinosaurs, as dynamic and successful animals. Although the important fossil track record of such diverse tetrapod groups as amphibians, synapsids, non-dinosaurian archosaurs, birds, and mammals should not be overlooked, dinosaur trackways have often been singled out as the best fossil footprint evidence available for illustrating the principles of locomotor and social behaviour of extinct animals (Thulborn 1990; Lockley 1991).

Despite important discoveries about the locomotion of other groups such as pterosaurs (see Section 4.1.14), the dino-centred view of the fossil footprint record remains defensible for several reasons. Dinosaurs were a diverse group, including bird-sized bipeds and quadrupeds larger than any other known terrestrial tetrapods. They are well known and had a stratigraphic range (Late Triassic to Late Cretaceous) spanning half of the entire history of tetrapods. It is also significant that dinosaur tracks have helped dispel many archaic myths about dinosaur locomotion, such as brontosaur sprawling, tail dragging, and swimming. Such simple yet radical reappraisals of behaviour are particularly effective in highlighting the utility of tracks as dynamic evidence of living animals.

This approach was demonstrated effectively by Alexander (1976) when he proposed a formula:

$$v = 0.25g^{0.5}.\, l^{1.67}.\, h^{-1.17}$$

for estimating the speeds (v) attained by dinosaurs and other animals (where g is gravitational acceleration, l stride length and h hip height estimated as 4 × foot length). Variations of this formula are sometimes used (Thulborn 1990). Alexander's paper contributed to a revival in vertebrate ichnology, and it was soon established that at least some dinosaurs (theropods) were capable of running at speeds up to 40 km/h (Farlow 1981). Despite claims to the contrary, there is little ichnological evidence for running among non-theropod dinosaurs.

An outline of known saurischian and ornithischian trackway morphology indicates clear systematic trends in the evolution of dinosaur locomotion across the spectrum from small bipeds to large quadrupeds in these two clades. Dinosaurs originated as small, fully erect, unspecialized bipeds. The oldest unequivocal assemblages of trackways of bipeds are attributed to small coelophysid-like theropod dinosaurs. Their trackways are consistently narrow, as are their predominantly tridactyl footprints, of which ichnogenus *Grallator* is the best-known example. Pace angulation is typically high (170–180°) indicating a trackway width (straddle) that barely exceeds the width of individual footprints (Fig. 4.1.11.1). Theropod tracks sometimes reveal metatarsal impressions. A few examples of wide-gauge trackways of large theropods are known. (Wide and narrow gauge refers to the width of the trackway and the space between footprints on either side of the trackway axis: Figs 4.1.11.1 and 4.1.11.2.)

Saurischian trackways

During the Late Triassic and Early Jurassic saurischian radiation, the evolution of large sauropodomorphs (prosauropods and sauropods) is expressed in the track record by a progressive increase in trackway width, a shortening of average step length relative to footprint size, and a secondary reversion to quadrupedal progression (Fig. 4.1.11.1).

Prosauropods occupy an intermediate morphological and evolutionary position between theropods and sauropods. This is clearly reflected in the morphology of their trackways, which range from small and bipedal (theropod-like) to large and quadrupedal (sauropod-like), as seen in the ichnogenera *Pseudotetrapodosaurus* and *Tetrapodosaurus*, respectively. The well-known ichnogenus *Otozoum* indicates a trackmaker capable of switching from bipedal to quadrupedal and from narrow- to wide-gauge progression (Lockley and Hunt 1995). The footprints are tetradactyl, a condition intermediate between the tridactyl morphology of theropods and the pentadactyl morphology of sauropods (Fig. 4.1.11.1).

Sauropod trackways clearly express the large, quadrupedal, wide-gauge, and wide-footed end of the saurischian spectrum. *Brontopodus* is the best-known ichnogenus, revealing a wide-gauge morphology. Pace angulations average 100–110° and trackway width is often two to three times the width of individual footprints. In contrast to theropod tracks, which have a central axis parallel to the trackway midline, sauropod footprint axes diverge anteriorly (Fig. 4.1.11.1). Also in contrast to theropod trackways, all speed estimates derived from sauropod tracks indicate slow walking progression.

Sauropod trackways include both wide- and narrow-gauge varieties, the latter assigned to ichnogenus *Parabrontopodus* (Lockley *et al.* 1994). Both originated in the early Mesozoic (Late Triassic to Early Jurassic), but wide-gauge locomotion predominates in the Cretaceous and has been linked to the brachiosaurid and titanosaurid clades. Wide-gauge trackways generally appear to have larger manus/pes ratios than narrow-gauge varieties.

The main conclusion to be drawn from this survey of saurischian trackways is that there is a systematic variation in locomotor style from one end of the spectrum (small bipeds) to the other (large quadrupeds), with narrow- and wide-gauge trackways, respectively. There is also an increase in the number of pes and manus digits from three to five, so that, in effect, the foot widens in unison with the increase in trackway width. Within each group (theropods, prosauropods, and sauropods) there are representatives that tend towards the narrow and wide ends of the spectrum. Thus the same size-related influences on locomotor style (trackway width) operated with similar ichnological expression in all three groups, a case of 'locomotor convergence'. The general trend is from obligatory or facultative bipeds (with small manus not used much or at all in locomotion) to obligatory quadrupeds with increasingly large manus, relative to size of pes.

Ornithischian trackways

The systematic variation in locomotor style in the saurischian clade also occurs in the ornithischian clade, but with subtle differences. The earliest purported ornithopod tracks (ichnogenus *Anomoepus*) from the Lower Triassic (Hitchcock 1858) indicate small facultative bipeds. These tracks resemble those of small theropods in size and in being functionally tridactyl, although a medially directed hallux impression may also be preserved. Ornithopod tracks differ, however, from theropod tracks in sometimes preserving an inwardly rotated pentadactyl manus impression. The medial axis of digit III points forward or slightly inward, and the footprint is generally as wide as or wider than long, owing to greater digit divarication (Fig. 4.1.11.2). Stride is also generally shorter than in theropods of equivalent size.

When considered collectively, these trackway parameters are representative of certain features that help to differentiate all ornithopod tracks and most ornithischian tracks from those of saurischians. The following generalizations are pertinent. All ornithischians (with the possible exception of scutellosaurids and pachycephalosaurids, whose tracks are unknown) were either obligatory or optional quadrupeds, whereas among saurischians this only holds for sauropomorphs. Most ornithischians have pes footprints that are as wide as or wider than long, with a tendency to rotate inwards, whereas saurischian pes tracks are longer than wide and, if rotated, face outward. Note, however, that in both groups the same pattern of increased outward rotation is observed as animals increase in size and move from bipedal to obligatory quadrupedal progression.

Well-known tracks of large ornithopods include the mid-Cretaceous ichnogenus *Caririchnium* which has an inwardly rotated, wider-than-long tridactyl pes, a short step, and a pace angulation of about 150°. Other large but unnamed Cretaceous iguanodontid and hadrosaurid tracks show similar morphological and locomotor characteristics.

Among thyreophorans, tracks of ancestral forms like *Scutellosaurus* are not known, and tracks attributable to stegosaurs have only recently been reported. These share with ornithopods the inwardly rotated tridactyl pes but have a much larger manus. Ankylosaurid pes tracks are tetradactyl and also have a large manus, and show little evidence of either inward or outward rotation of the manus or pes. Among ankylosaurids, trackway width is generally greater than in other large ornithischians, and this may be the only group that can be considered wide gauge on the basis of current trackway evidence.

Trackways of the last major group of ornithischians—the Marginocephalia (pachycephalosaurids and ceratopsids)—are poorly known. Pachycephalosaurids are unknown in the fossil footprint record, and ceratopsids are known from only a few localities where preservation is suboptimal and the trackway sample small. Ceratopsian tracks (*Ceratopsipes*) are somewhat similar to those of ankylosaurs (*Tetrapodosaurus*) but are evidently narrower gauge with respect to the pes, at least in some cases. The inner margins of the manus tracks are situated further from the midline than those of the pes suggesting a tendency towards a wide anterior straddle (Lockley and Hunt 1995; Dodson and Farlow 1997).

Conclusions

Comparison of the general pattern of ornithischian and saurischian ichnology suggests significant convergence. Both groups originated with small, unspecialized, predominantly tridactyl, narrow-gauge, sometimes crouching bipeds, and gave rise progressively to large, specialized, wider-gauge quadrupeds with larger front feet. Increased width is also expressed in increased number of digits. The same trends can be observed, to varying degrees, within the subclades that make up these two major divisions of the Dinosauria. When these locomotor characteristics are compared between the two groups, the tridactyl, carnivorous theropods occupy the extreme, exclusively bipedal end of the spectrum, and the herbivorous sauropomorphs are seen to be convergent with the herbivorous ornithischians as

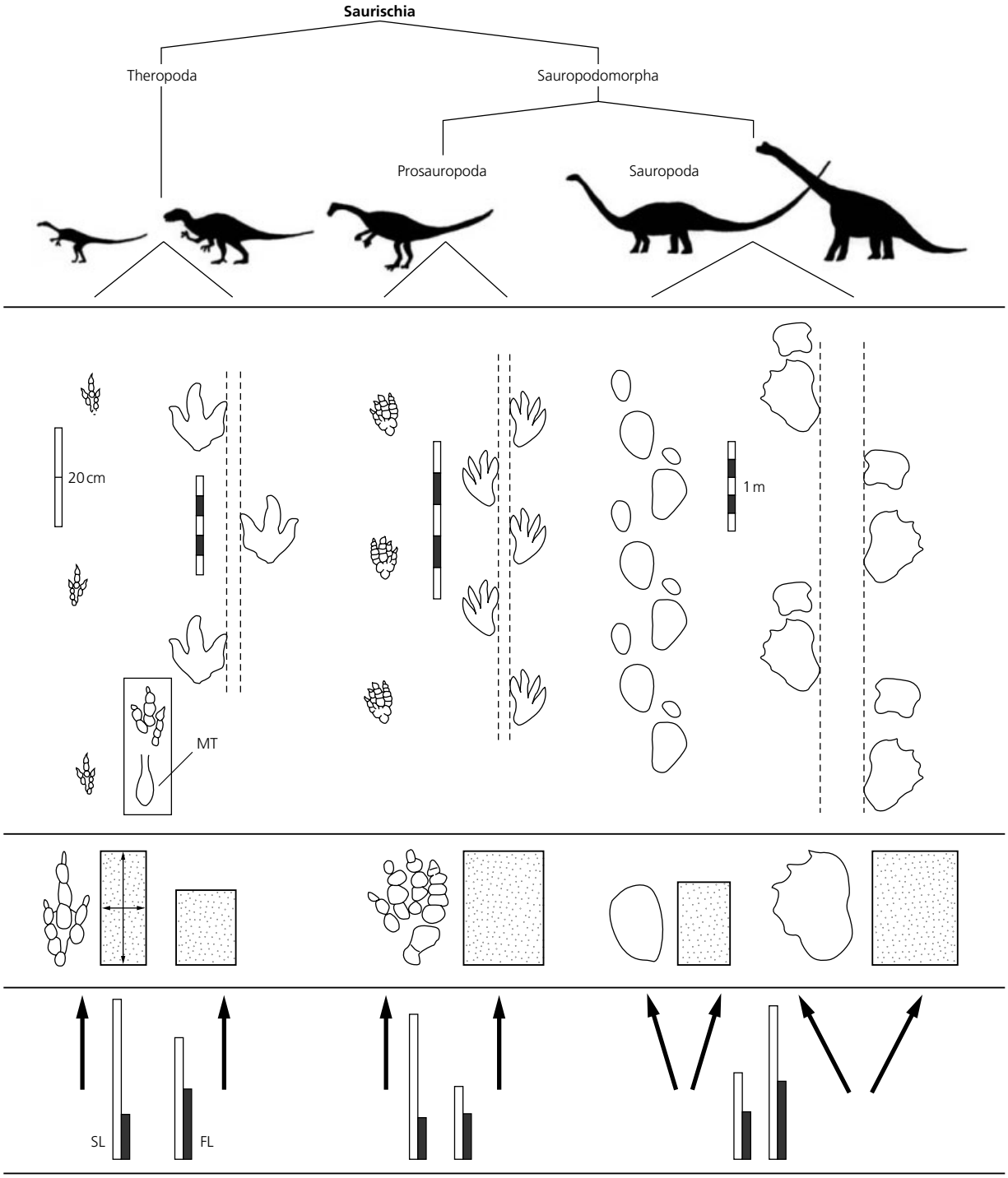

Fig. 4.1.11.1 Trackway configurations (centre) for main groups of saurischian dinosaurs (top), with inset showing theropod footprint with metatarsal impression (MT). From left to right, trackways are: *Grallator*, *Megalosauripus*, *Otozoum* (narrow-gauge), *Otozoum* (wide-gauge), *Parabrontopodus*, and *Brontopodus* (all based on type material). Scale bars = 1 m, except for *Grallator*. Note that all footprints are longer than wide (indicated by stippled rectangles which correspond to footprint length and width). Footprint axes (arrows) point forward or outward (bottom row), and step length/foot length ratios (SL/FL shown as white and black bars, respectively) decrease from left to right. (Compare with Fig. 4.1.11.2.)

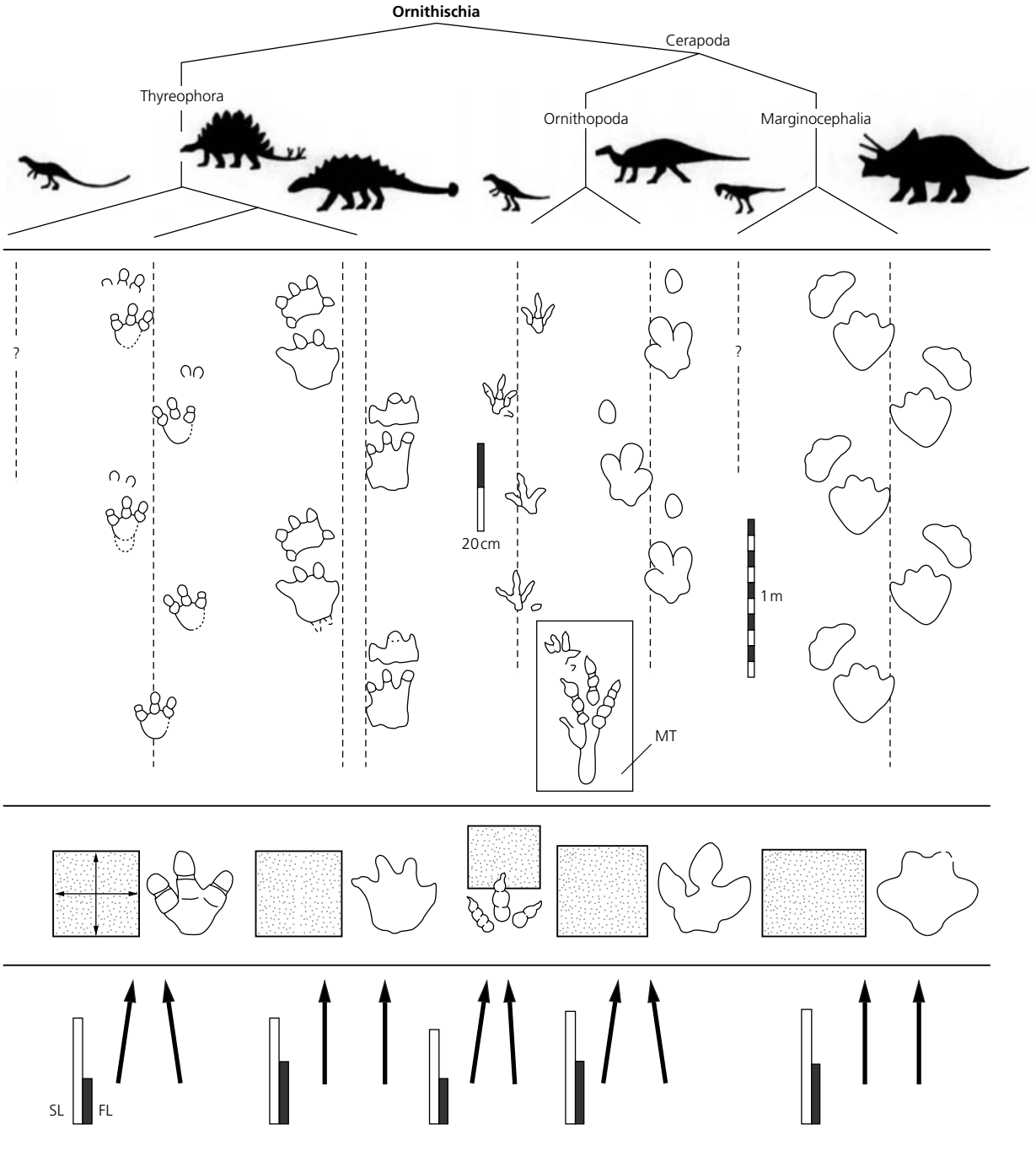

Fig. 4.1.11.2 Trackway configurations (centre) for main groups of ornithischian dinosaurs (top), with inset showing ornithopod footprint with metatarsal impression (MT). From left to right, trackways are: unnamed stegosaur trackway, *Tetrapodosaurus*, *Anomoepus*, *Caririchnium*, and *Ceratopsipes* (all based on type material). All at same scale except for *Anomoepus*. ?, no trackways known for scutellosaurids and pachycephalosaurids (see text for details). Note that all footprints are as wide as or wider than long (indicated by stippled rectangles which correspond to footprint length and width). Footprint axes (arrows) point forward or inward (bottom row), and step length/foot length ratios (SL/FL shown as white and black bars, respectively) decrease from left to right. (Compare with Fig. 4.1.11.1.)

tetradactyl and pentadactyl facultative and obligatory quadrupeds.

The reiterated or convergent patterns of increased width of both tracks and trackways across several dinosaur clades, and the clade Dinosauria as a whole, can be referred to as 'morphodynamic movements'. They are analogous to patterns of allometric growth in individuals of a species, or individuals of related species during ontogeny (or morphogenesis). Such recurrent and convergent developmental patterns, which are tied to heterochronic development (see Section 2.3.5), operate in clades at all taxonomic levels, i.e. above, as well as at, the species level, and in evolutionary as well as in ontogenetic time.

References

Alexander, R. McN. (1976) Estimates of speeds of dinosaurs. *Nature* **261**, 129–130.

Dodson, P. and Farlow, J.O. (1997) The forelimb carriage of ceratopsid dinosaurs. In: D.L. Wolberg, E. Stump and G. Rosenberg, eds. *Dinofest International*, pp. 393–398. Academy of Natural Sciences, Philadelphia.

Farlow, J.O. (1981) Estimates of dinosaur speeds from a new trackway site in Texas. *Nature* **294**, 747–748.

Hitchcock, E. (1858) *A report on the sandstone of the Connecticut Valley, especially its fossil footmarks*. W. White, Boston. (Reprinted in the Natural Sciences in America Series by Arno Press.)

Lockley, M.G. (1991) *Tracking dinosaurs*. Cambridge University Press, Cambridge.

Lockley, M.G. and Hunt, A.P. (1995) *Dinosaur tracks and other fossil footprints of the Western United States*. Columbia University Press, New York.

Lockley, M.G., Santos, V.F. dos, Meyer, C.A. and Hunt, A.P., eds. (1994) *Aspects of sauropod paleobiology*. Gaia: Revista de Geociencias, Museum Nacional de Historia Natural, no. 10. Lisbon, Portugal.

Thulborn, R.A. (1990) *Dinosaur tracks*. Chapman and Hall, London.

4.1.12 Dinosaur Ethology

J.R. HORNER

Introduction

Dinosaurs, like all other living and extinct animals, evolved a variety of behavioural life history strategies that helped to maximize the survival of their offspring. Because of the limits of the fossil record, however, only a few of the behaviours can actually be discovered or hypothesized, and these must be based on comparisons with behaviours known from living relatives. In short, hypotheses concerning dinosaur ethology are founded on interpretations made by comparing fossil specimens, in both geological and morphological contexts, with extant related taxa. Dinosaurs are archosaurs, and are thus closely related to living crocodilians. Birds share a common ancestor with the dromaeosaurid dinosaurs, and are also archosaurs (see Section 1.4.3). Interpretation of dinosaur behaviour, derived from either morphological or geological evidence, can be considered most reliable when the behavioural comparisons are made with living archosaurs.

Dinosaur eggs were hard-shelled, and although there are few that can be identified to particular taxa (Horner 2000) there exists no evidence to suggest live birth for any members of the Dinosauria (nor for any other members of the Archosauria). Species identification of eggs can only be verified by the discovery and identification of embryonic remains. In some instances, however, embryonic species identification is hampered by allometric changes that occurred during subsequent growth. Embryonic and juvenile dinosaurs can look very different from their adult counterparts (e.g. Horner and Currie 1994). The preservation of both egg and juvenile remains, and their taphonomic study, provide a basis for hypotheses concerning life history strategies.

Dinosaur behaviours that have been hypothesized from geological (taphonomic) and morphological data include nesting (nest construction, incubation, colonial nesting), parental care of young, and non-nesting gregarious behaviours (herding and packing).

Nesting

Clutch arrangement

Eggs attributed to dinosaurs, on the basis of either identification of embryos or inference from eggshell structure, are most often found in neatly arranged clutches. Individual eggs can vary from spherical to elongate in shape, with volumes that range from $\approx 500\,cm^3$ to $>5000\,cm^3$. Egg arrangements are most often circular, but some have been reported with paired linear rows, or globular clusters (Horner 2000). Some eggs, like the elongate asymmetrical eggs of the coelurosaurian *Troodon*, are found upright, having been pushed half their length into a fine silty sediment (Fig. 4.1.12.1). Statistical studies of *Troodon* clutches, and observations of clutches representing other dinosaurian taxa, reveal that the eggs were laid in pairs; this indicates that at least some dinosaurs had two functional, avian-like oviducts (Varricchio *et al.* 1997). These dinosaurs would have laid two eggs per day, or possibly over a longer period. The neatly arranged clutches, laid over an extended time interval, indicate considerable care in clutch arrange-

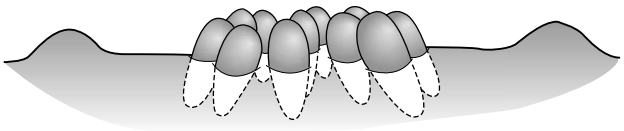

Fig. 4.1.12.1 Side view of a clutch of *Troodon formosus* eggs showing their relative position within the sediment, and the position of the soil rim found surrounding one of the clutches.

ment. Soil rims that skirt a clutch of *Troodon* eggs (Varricchio *et al.* 1997), and a group of juvenile *Maiasaura* (Horner 2000), show that some dinosaurs also built protective barriers around their nests.

Incubation

The discovery of adult specimens of *Troodon* and *Oviraptor* in direct association with partially buried egg clutches (Norell *et al.* 1995; Varricchio *et al.* 1997) indicates that these coelurosaurs extended parental attention in the form of brooding and/or egg protection. The fact that all dinosaur eggs discovered to date were at least partially buried indicates that the eggs did not have chalazae (the strand of fibrous albumen that holds bird yolks in position, allowing the eggs to be rolled around during incubation). Some eggs were completely buried and therefore incubated by external heat sources (e.g. solar).

Colonial nesting

Clutches of dinosaur eggs have been found at numerous sites around the world. In most instances a stratigraphic horizon yields numerous clutches which, based on their structural morphology, appear to be conspecific with one another (Horner 2000). Some of these associations extend over large (1 km^2) geographical areas. Extensive, associated, conspecific egg clutches imply that the nests were in colonies; the presence of large numbers of adults most likely improved the safety of both the eggs and hatchlings. Nesting horizons can be identified by the presence of abundant eggshell fragments, egg clutches, and the remains of juvenile skeletons and skeletal elements.

Parental care

In-nest care and growth

In rare instances, post-hatchling skeletons have been found in groups within the confines of nest-like structures, suggesting that some dinosaur hatchlings may have been altricial (nest-bound and dependent on the parents) for some time after hatching. A group of 15 post-hatchling juveniles (each 1 m long and postulated on the basis of morphological characters to be *Maiasaura peeblesorum*) possess skeletal elements that are very similar in size, suggesting synchronous hatching for this group of siblings. Hypothesized hatchling *Maiasaura* skeletons are 50 cm in length. A group of 15 20-cm long skeletons of *Protoceratops* from Mongolia also indicates synchronous hatching and a period of altriciality. Hatchling *Protoceratops* may have been about 10 cm in length.

Osteo-histological analyses show that pre- and post-hatchling maiasaurs and other hadrosaurs retained vast quantities of calcified cartilage in their long bones. Calcified cartilage provides rapid growth but is not strong enough to allow extended locomotion. Post-hatchling young, less than one-twentieth the size of adults and with paltry locomotor abilities, must have relied on parental care for protection and feeding. The duration of in-nest parental care can be hypothesized, based on increases in linear dimensions of the nesting juveniles and the bone depositional rates of known archosaurs. As the group of 15 post-hatchling maiasaurs had doubled in length from their hatchling size, and possess fibro-lamellar bone, depositional rates for these dinosaurs can be calculated, based on the known fibro-lamellar depositional rates of a duck (Castanet *et al.* 1996). These 1-m long maiasaurs were between 1 and 2 months old.

Post-nesting care and protection

Taphonomic studies on various dinosaur nesting horizons reveal the maximum size of the juvenile animals living in the colonies. Adult dinosaur specimens have not been found on any of the dinosaur nesting horizons; interestingly, no adult skeletal remains are found on the nesting grounds of the extant white pelican. Adult mortality is apparently very rare in nesting environments.

Skeletal elements, found on each of the maiasaur nesting horizons, include embryonic individuals ranging from 25 to 50 cm in length, and juveniles from 60 cm to 1.5 m. Although it is conceivable that all the relevant bones on the nesting horizon represent the remains of nest-bound, altricial young, it is also possible that the older juveniles left the confines of the nests, but remained in the nesting area in crèches or pods (Coombs 1989).

Numerous nests of the theropod dinosaurs *Troodon* and *Oviraptor* contain the uncrushed, hatched remains of eggs, indicating that the hatchlings left their nests at the time of hatching. Because post-hatchling juvenile skeletons are extremely rare, even on the nesting horizons, it is not known whether these dinosaurs protected their young after hatching.

Non-nesting gregarious behaviours

Juvenile associations

In addition to the groups of juvenile dinosaurs discovered either within nests or on nesting horizons, other groups have been found in non-nesting situations. The latter groups have been interpreted as recipients of some form of parental assistance, or as sibling pods (Coombs 1989).

Juvenile/adult associations

Monospecific or near monospecific associations of dinosaur remains, determined by taphonomic study to represent individuals that died at or near the same time, are relatively common in Cretaceous strata. Most of these monospecific associations are represented by plant-eating horned dinosaurs (ceratopsians) or duck-billed dinosaurs (hadrosaurs), and may comprise hundreds or even thousands of skeletons. Because these associations appear to represent cross-sections of natural populations that died together in either flood or drought conditions, it can be hypothesized that the animals also lived together. Hundreds or thousands of plant-eaters in a group must move from one area to another in order to have a constant supply of food, and thus can be interpreted as having travelled in herds or monospecific aggregations. Craniofacial structures, including horns, frills, and nasal protuberances on hadrosaurs and ceratopsians, have been interpreted as agnostic structures for use in hierarchical battles and sexual display (e.g. Sampson 1995).

Conclusions

Based on geological and morphological data, and comparisons with closely related extant taxa, a number of hypotheses can be proposed concerning the behavioural life history strategies of particular dinosaurs: (1) at least three species of hadrosaurs (*Maiasaura*, *Hypacrosaurus*, and an unidentified lambeosaurine) and one theropod taxon (*Troodon*) nested in colonies; (2) at least two taxa (*Maiasaura* and *Troodon*) constructed rimmed nests; (3) at least two taxa brooded their eggs (*Oviraptor* and *Troodon*); (4) at least two taxa (*Maiasaura* and *Protoceratops*) produced altricial hatchlings; and (5) numerous hadrosaur taxa (*Maiasaura*, *Prosaurolophus*, *Gryposaurus*, *Brachylophosaurus*, *Hypacrosaurus*, *Edmontosaurus*, and *Shantungosaurus*) and ceratopsian taxa (*Einiosaurus*, *Achaelosaurus*, *Centrosaurus*, *Styracosaurus*, *Pachyrhinosaurus*, and *Triceratops*) travelled in large, monospecific aggregations.

References

Castanet, J., Grandin, A., Abourachid, A. and de Ricqlès, A. (1996) Expression de la dynamique de croissance dans la structure de l'os périostique chez *Anas platyrhynchos*. *Comptes Rendus à l'Académie des Sciences, Paris (Sciences de la vie)* **319**, 301–308.

Coombs, W.P. Jr (1989) Modern analogs for dinosaur nesting and parental behavior. In: J.O. Farlow, ed. *Paleobiology of the dinosaurs*, pp. 21–53. Geological Society of America, Special Paper no. 238.

Horner, J.R. (2000) Dinosaur reproduction and parenting. *Annual Review of Earth and Planetary Sciences* **28**, 19–45.

Horner, J.R. and Currie, P.J. (1994) Embryonic and neonatal morphology and ontogeny of a new species of *Hypacrosaurus* (Ornithischia, Lambeosauridae) from Montana and Alberta. In: K. Carpenter, K. Hirsch and J.R. Horner, eds. *Dinosaur eggs and babies*, pp. 312–336. Cambridge University Press, Cambridge.

Norell, M.A., Clark, J.M., Chiappe, L.M. and Dashzeveg, D. (1995) A nesting dinosaur. *Nature* **378**, 774–776.

Sampson, S.D. (1995) Horns, herds and hierarchies. *Natural History* **104**, 36–40.

Varricchio, D.J., Jackson, F., Borkowski, J.J. and Horner, J.R. (1997) Nest and egg clutches of the dinosaur *Troodon formosus* and the evolution of avian reproductive traits. *Nature* **385**, 247–250.

4.1.13 Predatory Behaviour in Maniraptoran Theropods

A.D. GISHLICK

Introduction: extant predatory strategies

Many different prey capture methods are employed today by carnivores. The aim of a predator is to kill its prey without being injured or killed itself. Attacks are directed either to the rear or side of the prey, or they result in a 'quick kill' that reduces the potential for injury during combat with prey. These methods can be described and classified in many different complex ways, such as 'lurk and wait' or 'stalk and pounce' (Ewer 1973). However, two general classes of predatory behaviour are particularly apparent in situations where prey size is equal to or larger than the predator. These can be described as 'attack with jaws' and 'attack with claws'—essentially the predatory difference between dogs and cats. The 'jaw attack' strategy is employed, for example, by canids, hyaenas, crocodilians, sharks, and killer whales. The predator(s) pursues the prey, sometimes over long distances, biting repeatedly until the prey collapses. In some pack hunting, multiple predators bite

the extremities of the prey and hang on until the prey is dragged down (the method used by the African dog) (Ewer 1973). Predators that use the 'claw attack' lead with the forelimb and use the jaws to deliver a killing blow. This is the preferred method of felids, mustelids, baboons, preying mantis, and others. In this 'forelimb attack', the predator (typified by the cats) pounces on the prey and, clutching with both forelimbs, digs into the flesh with the claws. This blow either knocks down the prey, or the predator rakes backwards with its hindlimbs, dragging the prey over. The prey is then killed with bites to the neck and back of the head, or suffocated with bites to the face and throat (Ewer 1973).

Predatory strategies in theropods

Although theropods are unusual in that they were bipedal predators, they exhibit the same two prey capture strategies (Holtz 1994). Jaw attack theropods had large heads and short forelimbs. Some, such as tyrannosaurids, had highly reinforced skulls that may have been used to absorb forces involved in jaw to prey impact (Molnar and Farlow *in* Weishampel *et al.* 1990; Holtz 1994).

Theropods with relatively smaller skulls and longer forelimbs probably attacked with their forelimbs (Holtz 1994). These include herrerasaurids, oviraptors, troodontids, and dromaeosaurs (the last three being maniraptorans). Dromaeosaurs are the sister group to the flighted dinosaurs, Avialae, which include living birds (Aves) and their extinct flying relatives (Fig. 4.1.13.1). They had three attack components: clawed hands, teeth, and a raptorial pedal digit. The active lifestyle of this group is suggested by the long, powerful hindlimbs and stiffened tail, used as a dynamic stabilizer while running, jumping, and employing the raptorial toe (Ostrom *in* Weishampel *et al.* 1990).

Forelimb attack in dromaeosaurs

Dromaeosaurs attacked prey of equal size to or larger than themselves, using a forelimb attack. This is evidenced by Mongolian fossils of a *Velociraptor* in combat with a *Protoceratops* (Ostrom *in* Weishampel *et al.* 1990; Unwin 1995). The *Velociraptor* was 'caught in the act' of employing a forelimb attack. Its arms are around the head of the *Protoceratops*, with the 'killer claw' on the second pedal digit directed at the underside of the *Protoceratops*' neck (Unwin 1995). This particular death assemblage is reminiscent of a weasel attacking a slightly larger prey. After clutching its prey, the weasel tries to overbalance the victim by throwing itself to the side and slashing with its hindlimbs (Ewer 1973).

Pack hunting behaviour in dromaeosaurs

Fossil evidence supports the possibility of pack hunting behaviour in dromaeosaurs when they were attacking prey significantly larger than themselves. *Deinonychus* teeth and body fossils are frequently found associated with a single *Tenontosaurus*, an ornithischian two or more times the size of *Deinonychus* (Maxwell and Ostrom 1995). Multiple *Deinonychus* would have leaped at the tenontosaur and employed the forelimb attack. An analogy for the attack of a single *Deinonychus* during the fray is the method used by wolverines on reindeer. The wolverine jumps on to the reindeer's back and clutches with both forelimbs, literally 'riding' the prey while delivering vicious bites to the back, neck, and back of the head (Ewer 1973). *Deinonychus* would have added the raking killer claw.

Mechanics of a forelimb attack

The wolverine analogy, however, reveals nothing of the mechanism of the forelimb clutch/strike in *Deinonychus*. Non-avian maniraptors and avians share a 'semilunate' carpal which creates the automatic extension and flexion of the wrist with the movement of the forearm. This motion is a rudimentary form of the modern avian flight stroke (Gauthier and Padian *in* Hecht *et al.* 1985). Many

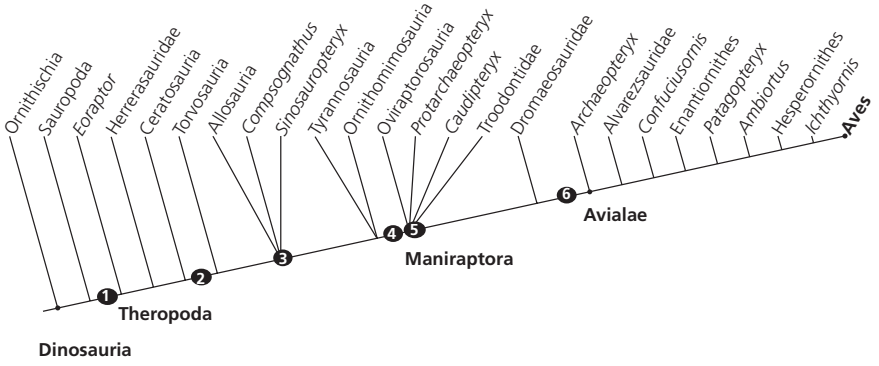

Fig. 4.1.13.1 Phylogeny of the Dinosauria, showing positions of the groups discussed, as well as some relevant characters and when they first appear. 1, 'Grasping' hands; 2, hand moves in flat plane; 3 , hair-like feather structures for insulation; 4, semilunate carpal, and origin of 'flight' stroke for grasping prey; 5, enlarged feathers on hands and tail; 6, flight feathers.

of the features of the avian flight mechanism were present in rudimentary form in *Deinonychus*.

Although the range of motion of the forelimb of *Deinonychus* was less than that of a modern bird, the overall action was the same (Gauthier and Padian *in* Hecht *et al.* 1985). First, the folded arms were held compact and close to the body. A rapid forward strike created by the extension of the humerus and elbow automatically unfolded the arm out from the body, then down and forward (downstroke). Pulling the humerus back and flexing the elbow folded the arm upward and in towards the body (upstroke) (Gauthier and Padian *in* Hecht *et al.* 1985) (Fig. 4.1.13.2). Watching bird wings flap in powered flight suggests just how fast this strike might have been. In view of its lack of a precision grasp, *Deinonychus* would have had to 'clutch' with both hands in unison in order to hold anything with its forelimbs.

When attacking smaller prey, the arms would have come from both sides and behind (out of the prey's vision) and drawn the prey towards the body of the predator with great speed. When attacking larger prey, the predatory strike motion allowed the arms to be extended wide, encompassing a sizeable volume of the prey while providing wide-spaced anchor points. Finally, the folding and rotation of the wrist during the upstroke would have drawn the claws up and in, locking them in the prey like the barbs of a harpoon, and attaching the predator firmly to its prey. This action would have been especially useful if *Deinonychus* engaged in wolverine-like 'riding' behaviour.

Predation and feathers

Discoveries in China have revealed that coelurosaurian theropods were feathered (Ji *et al.* 1998). *Protarchaeopteryx* and *Caudipteryx* had elongate, symmetrical feathers on the hands and tails (Ji *et al.* 1998). Surprisingly, these animals appear to be more primitive than dromaeosaurs. This implies that, primitively, dromaeosaurs also had elongate symmetrical feathers on their hands (see Fig. 4.1.13.1, point 5).

An examination of the hand of *Deinonychus* shows that feathers would not prohibit its use. Feathers on modern birds, and on *Archaeopteryx* and *Caudipteryx*, attach to the second finger of the hand. On the basis of phylogenetic bracketing, if *Deinonychus* had elongate feathers, they too would have attached to the second digit. The third finger of *Deinonychus'* hand would have been free of the attached feathers. Further, due to the angle of the hands during prey capture, feathers would not have impeded a forelimb attack (Fig. 4.1.13.3).

Feathers would give a number of potential advantages to the predator. Feathers on the hands could increase manoeuvrability while running, cornering, and braking (Peterson *in* Hecht *et al.* 1985), as well as control during leaps (Caple *et al.* 1983). When attacking smaller prey, feathers could be used as 'blinders', making the hands and arms appear larger, and thereby discouraging the prey from dodging to either side at the close of the strike. In a pack hunting situation, this same technique could be employed in a herding behaviour.

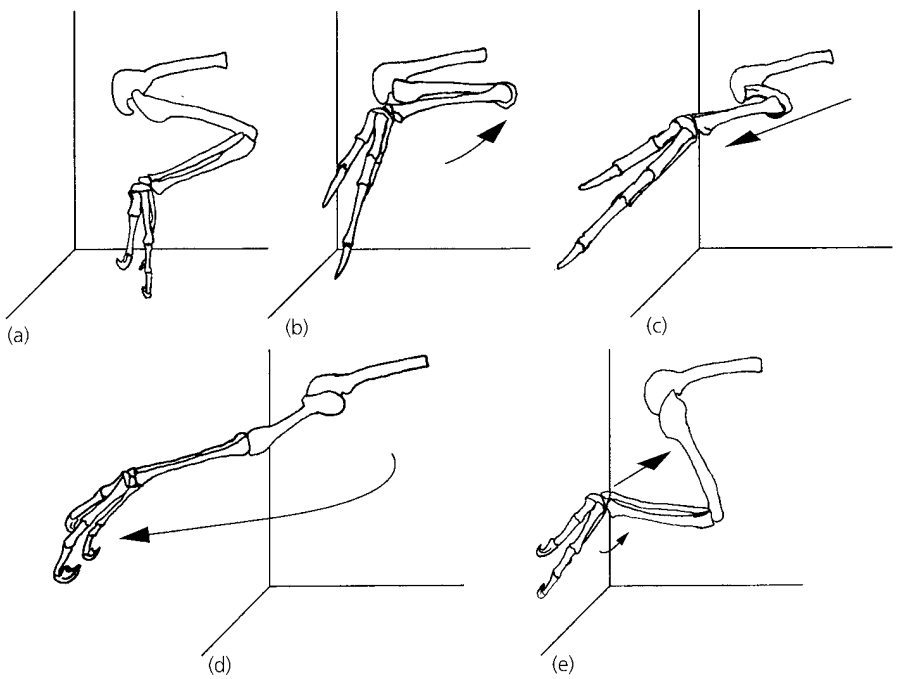

Fig. 4.1.13.2 Forearm and manus movements during a grasp/flight stroke of *Deinonychus*. (a) Arm folded in 'resting' position. (b) Rotation of shoulder, raising elbow (upstroke). (c) Extension of elbow, and resultant extension of manus (beginning of downstroke). (d) Forward sweep of arm (downstroke). (e) Flexion of elbow, and folding of wrist (beginning upstroke).

Fig. 4.1.13.3 (a,b) Hypothetical attachment of feathers on *Deinonychus*, based on *Caudipteryx* model; feathers attach to the second digit; note that the third digit is below the plane of the feathers and is thus usable. (c) *Deinonychus* grasping prey; angle of feathers does not impede the use of the manus or forearm.

Conclusion: predation and its relationship to flight

From phylogeny, it is evident that birds are living dinosaurs, descended from terrestrial, bipedal, cursorial predators (Fig. 4.1.13.1). It has been suggested that the flight stroke initially evolved as a predatory grasp, and was only later exapted for flight (Gauthier and Padian *in* Hecht *et al*. 1985). Indeed, the functional morphology of non-avian maniraptors shows that the arm motion during a forelimb attack was a rudimentary form of the basic flight stroke. Feathers would not have impeded the use of the hands in predation. Instead, feathers could have increased stabilization and maneouvrability while running, and added control and distance during leaps. Behavioural analogies to extant predators reinforce the idea that a forelimb attack might have been used for prey capture.

Throughout the transformation from predatory grasp to flight, functional continuity had to be maintained. The necessity of an efficient predation strategy would have resulted in the continued use and progressive modification of the grasping strike and the aerodynamic properties of feathers. At some point, the feather-covered arm would have been exapted for flight and subsequently refined to the mechanism in birds today. Thus longer, more aerodynamic feathers and a forelimb attack may have gone hand in hand, allowing cursorial, leaping predators to graduate to flight.

References

Caple, G., Russel, P.B. and Willis, W.R. (1983) The physics of leaping animals and the evolution of preflight. *American Naturalist* **124**, 455–467.

Ewer, R.F. (1973) *The carnivores*. Cornell University Press, Ithaca.

Hecht, M., Ostrom, J.H., Viohl, G. and Wellnhofer, P., eds. (1985) *The beginnings of birds.* Proceedings of the International Archaeopteryx Conference Eichstätt, 1984.

Holtz, T.R.J. (1994) Predatory adaptions of the skull and unguals of modern and extinct carnivorous amniotes. *Journal of Vertebrate Paleontology* **14**, 29–30A.

Ji, Q., Currie, P.J., Norell, M.A. and Ji, S.-A. (1998) Two feathered dinosaurs from northeastern China. *Nature* **393**, 753–761.

Maxwell, W.D. and Ostrom, J.H. (1995) Taphonomy and paleobiological implications of *Tenontosaurus–Deinonychus* associations. *Journal of Vertebrate Paleontology* **15**, 707–712.

Unwin, D.M. (1995) *Protoceratops* and *Velociraptor* preserved in association: evidence for predatory behavior in dromaeosaurid dinosaurs. *Journal of Vertebrate Paleontology* **15**, 57–58A.

Weishampel, D.B., Dodson, P. and Osmólska, H., eds. (1990) *The Dinosauria*. University of California Press, Berkeley.

4.1.14 Pterosaur Locomotion

D.M. UNWIN

Introduction

Pterosaurs were a diverse group of highly derived diapsid reptiles, and the first vertebrates to achieve true flapping flight. Known from the Late Triassic through to the end of the Cretaceous, pterosaurs had spread world-

wide by the Early Jurassic and remained the dominant aerial vertebrate for much of the rest of the Mesozoic. Pterosaurs were of relatively light construction, and consequently their fossil record is poor and highly biased. The vast majority of remains have been recovered from just a few Lagerstätten restricted to marginal marine and marine environments (principally the Late Triassic Zorzino Limestone of Italy, the Early Jurassic Holzmaden Shales and Late Jurassic Solnhofen Limestone of Germany, the Early Cretaceous Santana Formation of Brazil, and the Late Cretaceous Niobrara Chalk of Kansas). A little over 100 species of pterosaur have been described, but of these only 30 or so are known from reasonably complete fossil remains (Wellnhofer 1991).

There are two principal morphotypes: 'rhamphorhynchoids' (paraphyletic) were less derived, with a more reptilian-like skull, a long tail, and a well-developed fifth toe in the foot; pterodactyloids were more derived, with a rather bird-like skull, a short tail, and, in most cases, no fifth toe. The majority of known species appear to have fed on fish, and the development of a tooth-grab, designed for snatching prey from the water surface, arose in at least four different lineages. A number of pterosaurs became filter-feeders, while others were highly specialized aerial insectivores. Most Triassic and Jurassic pterosaurs were less than 1 m in wingspan, though some 'rhamphorhynchoids' may have reached 2.5 m. By contrast, there were very few small pterosaurs in the Cretaceous; most species ranged from 3 to 6 m in wingspan, but wingspans of 9–12 m were reached in two separate lineages.

Flight apparatus

The flight apparatus consisted principally of the flight membranes and supporting limbs (Fig. 4.1.14.1), but other structures, including an elongate tail bearing a terminal flap (found only in 'rhamphorhynchoids'), foot webs, and cranial crests, may also have played important roles. Muscles, nervous control, and physiology were also directly involved in flight, but the fossil evidence for these is strictly limited, and such systems are still poorly understood.

The flight surfaces consisted of thin sheets of membrane derived from the integument. Well-preserved specimens from Kazakhstan and Brazil show that the membranes were multilayered and composed of a thin epidermis, a vascular layer, wing fibres, and, at least in some regions near the body, muscle fibres (Martill and Unwin 1989). The wing fibres were long, fine, rod-like structures, generally about 0.05–0.1 mm in diameter (Fig. 4.1.14.2); they were distributed throughout the wing membranes, endowing them with structural integrity and helping to maintain their shape (Padian and Rayner 1993).

The extent of the flight membranes and their degree of attachment to the limbs and body have been disputed, but well-preserved wings of the Late Jurassic pterosaurs *Sordes*, *Rhamphorhynchus*, and *Pterodactylus* have resolved the major questions (Unwin and Bakhurina 1994). An anterior flight surface, the propatagium, was located in the angle between the humerus and forearm and was supported distally by the pteroid. The main flight surface, or brachiopatagium, was attached to the rear edge of the elongated forelimb, to the lateral surface of the body from the shoulder to the pelvis, and to the anterior surface of the hindlimb as far as the distal end of the crus. In 'rhamphorhynchoids' there was a large cruropatagium stretched between the hindlimbs and supported by the fifth toe of the pes, but not attached to the tail. In pterodactyloids this posterior flight surface was reduced in size and divided into two, one panel located in the inner angle of each leg (Fig. 4.1.14.1).

Flight ability

Various lines of evidence indicate that pterosaurs were true flapping fliers rather than gliders (Wellnhofer 1991).

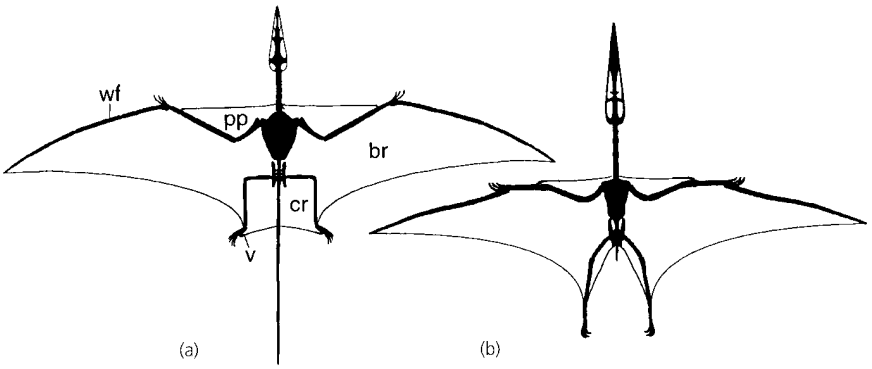

Fig. 4.1.14.1 Restoration of the skeleton and wing membranes of pterosaurs. (a) The 'rhamphorhynchoid' pterosaur *Sordes* (wingspan 0.5 m) from the Upper Jurassic of Kazakhstan. (b) The pterodactyloid *Pterodactylus* (wingspan 0.4 m) from the Upper Jurassic of Germany. Abbreviations: br, brachiopatagium; cr, cruropatagium; pp, propatagium; v, digit 5 of pes; wf, wing-finger.

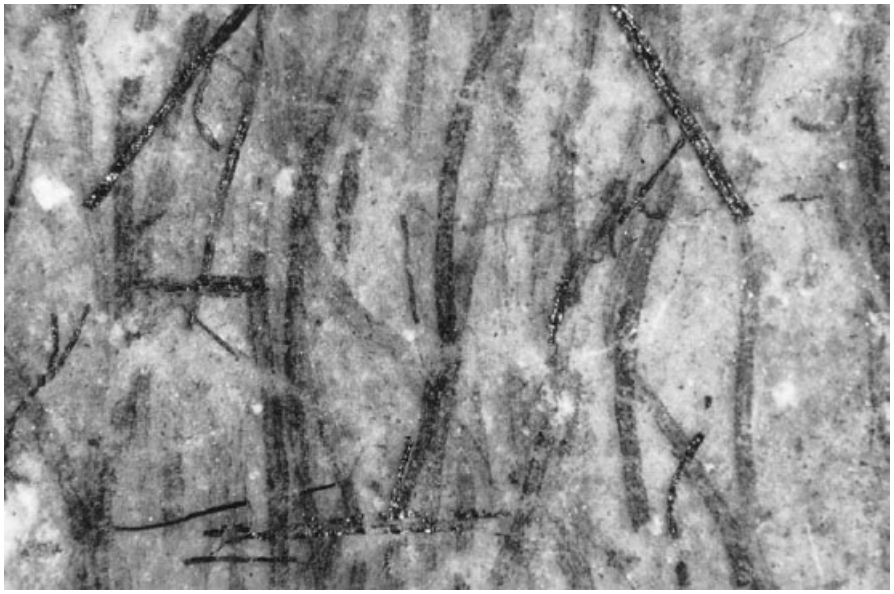

Fig. 4.1.14.2 Wing fibres of *Sordes pilosus* from the Upper Jurassic of Karatau, Kazakhstan. The fibres are typically ≈ 80 µm in width.

The construction of their joints ensured an efficient flight stroke, and processes and scars on their limb bones indicate the presence of flight muscles of more than sufficient size to power the flap cycle. Their flight surfaces were sophisticated structures that could be cambered and orientated to produce lift, thrust, and directional control. Adaptations for aerial insectivory and the discovery of remains in marine sediments deposited hundreds of kilometres from land also indicate considerable aeronautical ability, far beyond that of typical gliders.

It seems likely that the flight stroke was similar to that of birds and bats, with both fore and hind limbs following a similar pathway: a forward and downward power stroke followed by an upward and backward recovery stroke. Pterosaurs could exert considerable control over the shape and orientation of their flight surfaces. By elevating and depressing the pteroid, the propatagium was employed as an anterior flap, enabling cambering of the wing during slow flight, landing, and take-off. Movements of the fore and hind limbs were used to change the shape and camber of the brachiopatagium, and movements of the fifth toe permitted some independent manipulation of the cruropatagium, enabling it to be used for manoeuvring and braking. With their relatively large wings and light construction it seems likely that pterosaurs had a lower wing loading than birds of a similar size. This indicates a somewhat slower stall speed, making landing and take-off easier. Pterosaurs were probably relatively slow, manoeuvrable fliers, as might be expected for aerial insectivores and piscivores.

While pterosaurs, especially small to medium forms, probably depended primarily on powered flapping flight, in many species wing shape was well suited to soaring and it is likely that most (perhaps all) pterosaurs took advantage of this to save energy. Large and giant forms neared the limit of what was possible in terms of energetics and may have spent much of their time soaring. Large forms such as *Pteranodon* seem to have been extremely well adapted in this respect and were probably able to exploit thermals, wave soaring, and relief lift (upcurrents over hills and cliffs) in order to reduce the energetic cost of staying aloft. Like some modern ocean-going birds, such as the albatross, *Pteranodon* and related forms were probably capable of flying remarkably long distances.

Terrestrial ability

In recent years there has been much dispute over the terrestrial ability of pterosaurs. It has been argued, contrary to traditional views, that pterosaurs were bird-like, with a fully erect, bipedal, digitigrade stance and gait. However, there is a growing body of evidence from anatomical studies and reanalysis of trackways that pterosaurs were quadrupedal plantigrades, as previously thought (Unwin 1997).

Complete, uncrushed remains from the Santana Formation of Brazil show that when large pterodactyloids such as *Anhanguera* stood on the ground, the femur was angled outward and downward, while the lower leg was directed vertically (Fig. 4.1.14.3). Unlike birds, the construction of joints in the foot did not permit the extreme extension of the digits that allows the metatarsus to be raised off the ground; thus pterosaurs were obligatory plantigrades. The hindlimb step cycle was largely effected by flexion and extension of the lower leg, com-

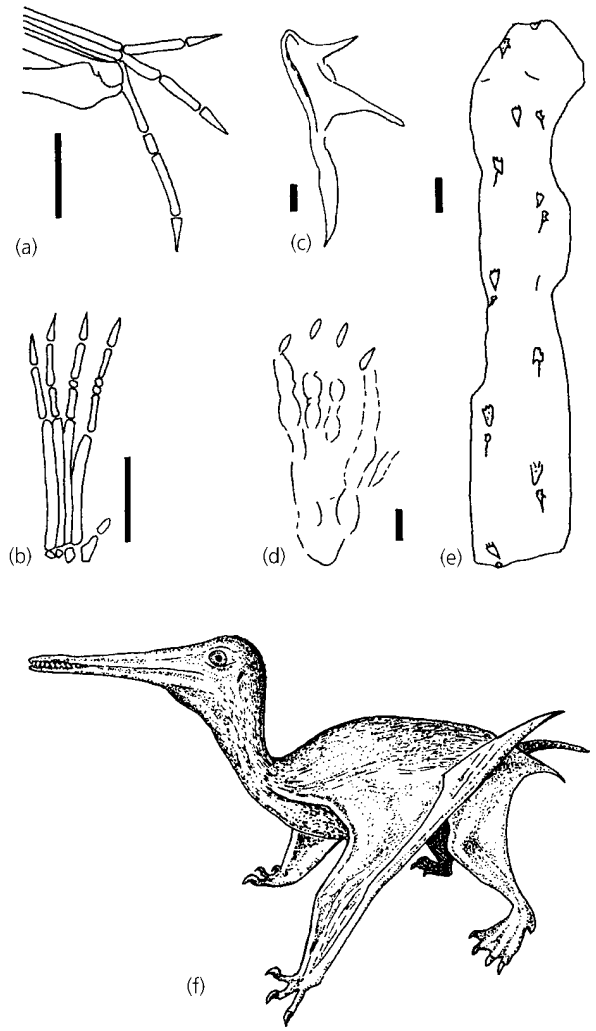

Fig. 4.1.14.3 (a,b) Manus and pes of *Pterodactylus*. (c,d) Manus and pes prints of the pterosaur ichnogenus *Pteraichnus*. (e) *Pteraichnus* from the Jurassic of Arizona. (f) *Pterodactylus* restored as a quadrupedal plantigrade. Scale bars: (a–d) 10 mm; (e) 100 mm. (a–e, From Unwin 1997.)

bined with some protraction and retraction of the femur. The anterior half of the body was supported by the forelimbs, with the manus facing outward and somewhat to the rear and the wing-finger folded up toward the body (Fig. 4.1.14.3).

Details of trackways referred to the ichnogenus *Pteraichnus* from more than 20 localities in America, Europe, and Asia, ranging in age from late Middle Jurassic to Late Cretaceous (Unwin 1997), are completely consistent with pterosaur anatomy. They confirm that pterosaurs moved in quadrupedal plantigrade fashion (Fig. 4.1.14.3). Despite the apparent awkwardness of this type of gait, the trackways suggest that it was reasonably efficient; pterodactyloid pterosaurs, at least, may have had an effective terrestrial ability. The chaotic distribution of prints and presence of 'beak-marks' suggest that some trackway assemblages were produced by flocks of pterosaurs feeding on mud flats.

Other locomotory abilities

With the likely exception of larger forms, most pterosaurs were probably capable of climbing trees or cliffs, supported by the clawed digits of the first three fingers of the hand and digits 1–4 of the foot. Early pterosaurs seem to have been well equipped in this respect and it may be that, when not airborne, 'rhamphorhynchoids', with their long tails and large cruropatagia, were predominantly arboreal. This behaviour was probably plesiomorphic for pterosaurs, in that pterosaur flight is likely to have evolved through a gravity-assisted gliding phase, using high-starts from trees or cliffs.

It has occasionally been suggested that pterosaurs were able to swim in gull-like fashion on the water surface, or perhaps even to dive for prey items. While such activities cannot be ruled out entirely, the basic design of pterosaurs seems ill-suited for such purposes, although most species, especially the piscivorous forms, probably had some swimming ability and were no doubt able to take off from the water surface.

References

Martill, D.M. and Unwin, D.M. (1989) Exceptionally well-preserved pterosaur wing membrane from the Cretaceous of Brazil. *Nature* **340**, 138–140.

Padian, K. and Rayner, J.M.V. (1993) The wings of pterosaurs. *American Journal of Science* **293A**, 91–166.

Unwin, D.M. (1997) Pterosaur tracks and the terrestrial ability of pterosaurs. *Lethaia* **29**, 373–386.

Unwin, D.M. and Bakhurina, N.N. (1994) *Sordes pilosus* and the nature of the pterosaur flight apparatus. *Nature* **371**, 62–64.

Wellnhofer, P. (1991) *The illustrated encyclopedia of pterosaurs*. Salamander Books, London.

4.1.15 Predation in Sabre-tooth Cats

B. VAN VALKENBURGH

Introduction

Although they appear bizarre, sabre-tooth predators have been among the most successful forms to evolve over the course of mammalian history. They are an excellent example of convergent evolution, having evolved independently at least five times, once in marsupials, creodonts (an extinct order), and nimravids (an extinct family), and probably twice in the cat family Felidae.

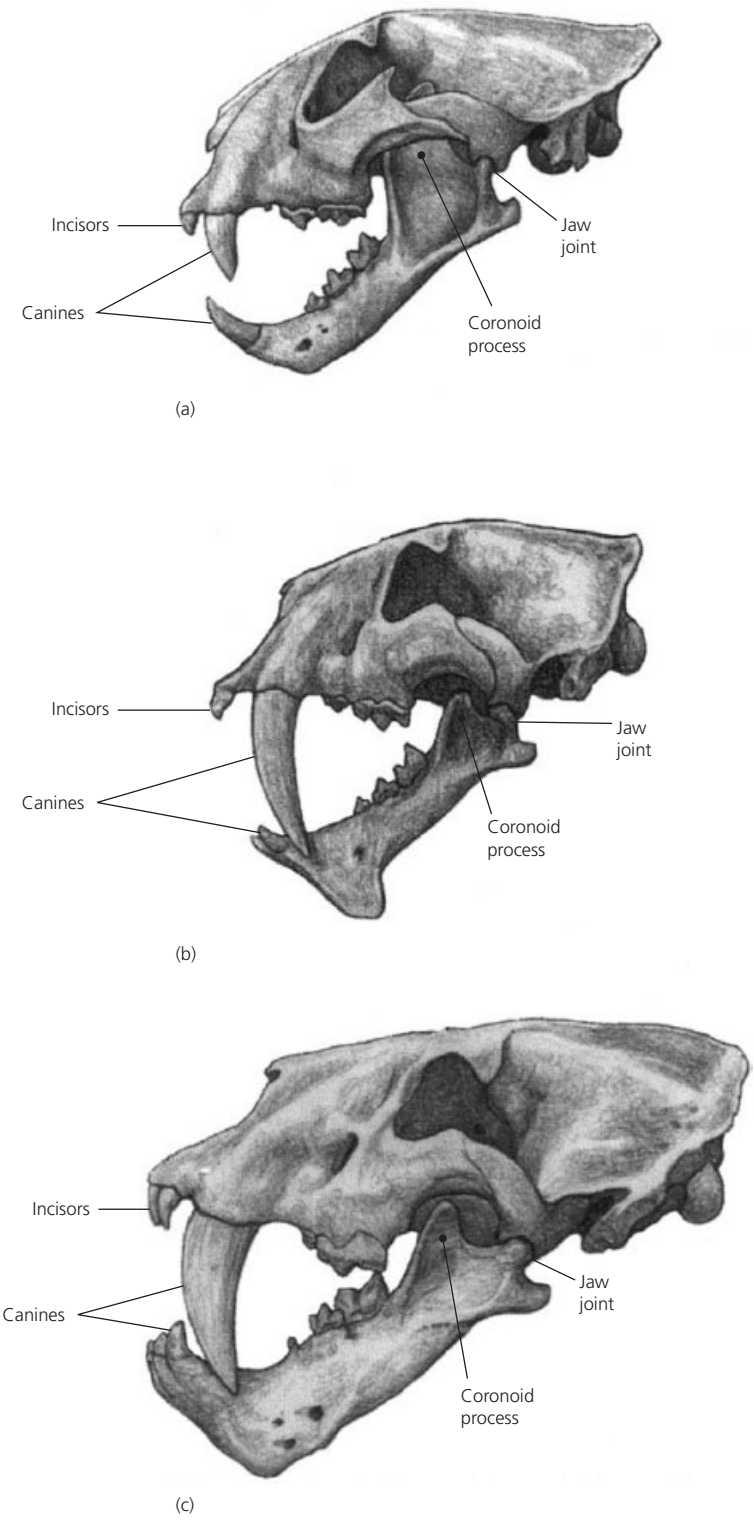

Fig. 4.1.15.1 Profile views of big cat skulls. (a) An extant conical tooth cat, the leopard. (b) Extinct smilodontine cat, *Megantereon*. (c) Extinct homothere, *Homotherium*. Note the size and position of the incisors and canines, the size of the coronoid process, and the position of the jaw joint relative to the tooth row. (From *The big cats and their fossil relatives*, by Alan Turner and Mauricio Anton (Contributor) © 1997, Columbia University Press. Reprinted with the permission of the publisher.)

From approximately 50 Ma until the latest Pleistocene, a sabre-tooth predator could be found somewhere on the planet, and they were the dominant big cat-like carnivores in the Old and New World until about 2 Ma. Given their widespread distribution and repeated appearance, it is clear that sabre-tooths were successful predators, but how they actually hunted and killed remains a subject of some debate.

Smilodontines and homotheres

Among the best-known sabre-tooths are those within

the family Felidae, designated as smilodontines and homotheres (Fig. 4.1.15.1). Smilodontines (e.g. *Smilodon*) had very long sabres that are narrow from front to back and display weak serrations. Homotheres (e.g. *Homotherium*) had somewhat shorter but broader sabres, with more prominent serrations. In some of the last representatives of each type of cat, the canine tooth differences were associated with marked differences in limb morphology; homotheres had longer, more gracile limbs than the stocky, robust smilodontines (Anyonge 1996; Turner and Anton 1997).

Both smilodontines and homotheres shared a number of features in their skulls and teeth that distinguish them from extant felids (Fig. 4.1.15.1). In addition to laterally compressed rather than round upper canine teeth, sabre-tooth cats had relatively larger incisor teeth that were set in a somewhat curved rather than straight row. The incisors projected anterior to the sabres and each tooth was more conical than the small, nearly spatulate incisors of today's cats. Sabre-tooth cats had very few cheek teeth, but of those remaining, the primary slicing tooth (carnassial) was enlarged. To allow their jaws to open wide enough to free the upper canines for a bite, the jaw joint of sabre-tooth cats was lower relative to the tooth row than that of extant felids. In addition, the coronoid process of the mandible was greatly reduced in sabre-tooths. This bony prong served as the lever arm for the primary jaw-closing muscle (temporalis); its reduction necessarily resulted in a lesser mechanical advantage for the muscle but prevented overstretching of the muscle during wide gapes. To compensate for the loss in jaw-closing force, sabre-tooth cats had an enlarged temporalis and recruited other muscles to assist in closure. More specifically, the muscles that run from the neck vertebrae to the base of the skull and act to pull the head downwards were enhanced. To close their jaws, sabre-tooths used a combination of powerful head depression and jaw elevation. Although extant felids have the same head-depressing musculature, it is not nearly as well developed and jaw elevation is the major action that produces a bite.

Sabre-tooth prey

Two major questions arise concerning sabre-tooth cat predation: (1) what did they eat; and (2) how did they kill? Like modern big cats, sabre-tooths probably took prey larger than themselves. Perhaps because of their huge canine teeth, they are often illustrated attacking extremely large and thick-skinned extinct animals, such as mammoths and ground sloths. It is doubtful that such enormous prey was the typical choice, because of both their relative rarity and the danger of injury to the predator. Sabre-tooth cats came in a variety of sizes; the smallest was leopard-size and the largest more massive than the largest tigers. However, most were approximately lion-size, and consequently would have preyed upon whatever wildebeest- to buffalo-size herbivores were readily available. For example, in the North American Pleistocene, there were large herds of horses, camels, and bison that probably sustained *Smilodon*. However, juvenile proboscideans might have been a preferred prey item for some sabre-tooths. Evidence for this comes from a cave in Texas that preserves the remains of 33 juvenile and adult *Homotherium* with those of more than 30 juvenile mammoths (Marean and Eberhardt 1995). The mammoth bones exhibit tooth marks and are mostly disarticulated limbs, suggesting that the homotheres brought the bones to the cave. Unfortunately, it is not possible to ascertain whether *Homotherium* killed the young proboscideans or merely scavenged from natural deaths. Since mammoths, like extant elephants, may have defended their young vigorously, taking a juvenile was probably very risky.

Given their stocky build, most sabre-tooths probably ambushed their prey, running a relatively short distance before making contact. The possible exception to this scenario is *Homotherium serum* whose long front legs and sloping back suggest greater running abilities (Anyonge 1996; Turner and Anton 1997). Notably, the gracile homotheres often coexisted with more robust smilodontines, and the two probably occupied somewhat different habitats, much as lion and leopard do today. Presumably homotheres inhabited more open areas, while smilodontines worked the forest edge.

The killing bite

The nature of the killing bite has puzzled palaeontologists for years. First, where was the bite best placed? Abdomen? Neck? Throat? And second, how was the actual kill made? Was it by massive blood loss due to repeated bites, or by a single crushing bite (as is typical of modern big cats)? Recent studies of tooth fracture frequency in felids, and a better understanding of sabre-tooth cat anatomy, have led to greater agreement concerning the killing bite.

The choice of where to place the killing bite was probably determined largely by the need to immobilize potentially dangerous prey as quickly as possible without breaking the slender upper canines. A sabre without its distal third or half would lose much of its tapered shape, making it much more difficult to drive through skin and muscle. By contrast, because modern big cats often kill by strangling or suffocating prey, their conical teeth can produce death grips even when blunted. A study of modern lions revealed that many individuals survived for years with at least one broken canine tooth. Based on the large sample of carnivores preserved in the Rancho La Brea tar pits of California, it

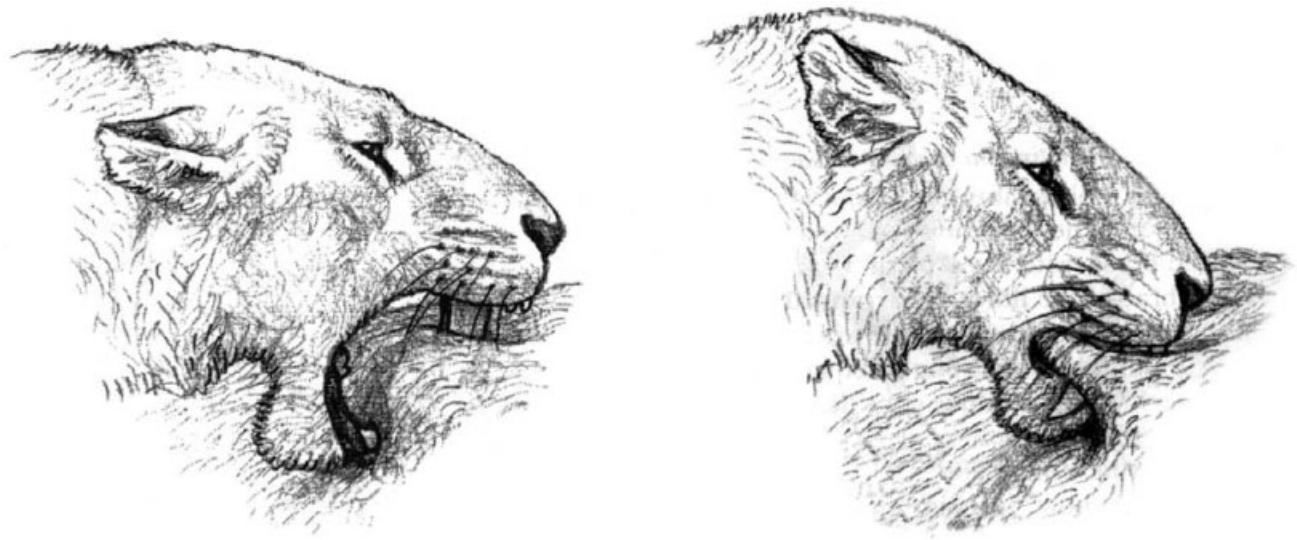

Fig. 4.1.15.2 Canine-shear killing bite of *Smilodon*, as proposed by Akersten (1985). (From *The big cats and their fossil relatives*, by Alan Turner and Mauricio Anton (Contributor) © 1997, Columbia University Press. Reprinted with the permission of the publisher.)

is clear that *Smilodon* broke its canines regularly, but less frequently than the large lion (*Panthera atrox*) with which it coexisted (Van Valkenburgh and Hertel 1993). To avoid canine fracture, sabre-tooths would have directed their bites toward areas of the body where contact with bone was unlikely. Two areas appear best: the abdomen and the ventral throat. The throat was probably preferred because a bite there could more easily sever critical vessels and nerves. In addition, the abdomen might be more problematic because it is partially obstructed by the hindlimb of the prey and the large ribcage that is typical of herbivores. In either case, sabre-tooths would have held prey immobile or nearly so with their heavily muscled forelimbs and protracted claws while they applied their canines to make the kill.

The bite itself would have depended on a strong downward pull on the cranium to drive the upper canines through the throat while the lower jaw was pulled upwards. The canines and enlarged incisors could work together to pinch a sizeable fold of flesh (Fig. 4.1.15.2) that would then be removed by a rearward pull of the head (Akersten 1985). The necks of sabre-tooth cats tend to be long and heavily muscled and were no doubt important in stabilizing the head during the killing bite as well as pulling backwards and downwards. The bite strength of a sabre-tooth was likely greater than that of living big cats. A recent study of the cross-sectional geometry of the mandible of *Smilodon* revealed it to be similar in strength and rigidity to that of living spotted hyaenas, animals that are known for their powerful bone-cracking jaws (Biknevicius and Van Valkenburgh 1996). Whether the kill required a single bite or multiple bites may have depended on the size of the prey. A smaller sabre-tooth taking a very large prey might need to use several bites to produce the necessary blood loss or sever the trachea. Although it is possible that sabre-tooth cats could have used a stranglehold, as do modern big cats, this seems unlikely, given the knife-like nature of their canine and incisor teeth. These were teeth shaped for slashing and ripping, rather than crushing and holding.

References

Akersten, W.A. (1985) Canine function in *Smilodon* (Mammalia; Felidae; Machairodontinae). *Los Angeles County Museum Contributions in Science* **356**, 1–22.

Anyonge, W. (1996) Locomotor behaviour in Plio-Pleistocene sabre-tooth cats: a biomechanical analysis. *Journal of Zoology* **238**, 395–413.

Biknevicius, A. and Van Valkenburgh, B. (1996) Design for killing: craniodental adaptations of predators. In: J.L. Gittleman, ed. *Carnivore behavior, ecology, and evolution*, Vol. II, pp. 393–428. Cornell University Press, Ithaca.

Marean, C.W. and Eberhardt, C.L. (1995) Paleoanthropological and paleoecological implications of the taphonomy of a sabre-tooth's den. *Journal of Human Evolution* **29**, 515–547.

Turner, A. and Anton, M. (1997) *The big cats and their fossil relatives*. Columbia University Press, New York.

Van Valkenburgh, B. and Hertel, F. (1993) Tough times at La Brea: tooth breakage in large carnivores of the late Pleistocene. *Science* **261**, 456–459.

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4.1.16 Plant–Animal Interactions: Herbivory

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Introduction

Despite the fact that animals have fed on land plants for at least 400 million years, there is remarkably little unequivocal evidence linking specific herbivores with specific plants. The nature of the fossil record ensures that most conclusions about herbivory are based on indirect evidence, indicating only that the activity took place or that certain organisms were herbivorous. Usually the plant-feeder and plant can be identified only in very general terms, in some instances by analogy or inference. Conclusions based on such indirect evidence can be open to question. In such cases reconstructions of food chains and energy flow in ancient ecosystems, and hypotheses about coevolution of plants and herbivores, are somewhat speculative.

Nature of the evidence

Evidence of herbivory in the geological record takes many forms, some of which establish herbivore–plant relationships more precisely than others. Fossilized gut contents within the body cavities of herbivores provide the strongest evidence, while identifiable remains of vegetation found stuck to and between teeth also clearly link herbivore and diet. However, such direct evidence of herbivory is found only in very special geological circumstances. More common but less informative is the evidence provided by coprolites. The coprolites of herbivores, however, must be distinguished from those of detritivores (consumers of dead plant matter) (Taylor and Taylor 1993).

Plant-bearing coprolites are comparatively rare in the geological record because the excrement of herbivores, in contrast to that of carnivores, is relatively fragile and often disintegrates before it can be incorporated into sediment. Plant-bearing coprolites produced by tetrapods are generally oval to fusiform in shape and 1–500 mm in diameter; those produced by arthropods are usually smaller. Coprolites occur as discrete bodies in sediment or attached to a substrate, such as leaves or wood fragments; they can also occur in wood borings. The evidence for herbivory which can be derived from coprolites is rather limited because few recognizable plant remains survive digestion. Only those parts composed of relatively stable materials endure, such as bits of thick cuticle, palynomorphs, and tracheids. More delicate plant organs (e.g. reproductive structures) and the remains of delicate plants (e.g. ferns) may not be recognizable at all, even though the herbivore ingested large amounts of such material. Although the size, shape, and contents of coprolites can point to a particular group, they cannot usually be assigned to a specific herbivore. Nevertheless, when the available evidence is linked with the geological environment in which the coprolites are found, it may be possible to determine their source. By using such information some coprolites can be attributed to specific herbivores, ranging from mites to dinosaurs and humans, with some confidence.

Less direct evidence can be derived from external bite marks, leaf mines, borings, and wound tissue. The mouthparts of insects and the teeth and jaw structures of vertebrates can be used to identify herbivores and the feeding techniques that they employed. However, it usually is not possible to determine which plants such insects or vertebrates ate, except in very general terms. For example, it can be assumed that most Late Cretaceous and Cenozoic herbivores fed on angiosperms because they have been the dominant plants in most terrestrial environments since about the middle of the Cretaceous. Earlier herbivores must have fed on some combination of pteridophytes and gymnosperms, depending on availability. In a few circumstances (see below) it has proved possible to confirm the diet of certain dinosaurs and mammals which had been inferred previously from a study of their teeth.

Herbivory in arthropods

Most of our knowledge of herbivory in arthropods comes from coprolites, feeding marks on leaves and other plant parts, wood borings (sometimes containing coprolites), and inferences based on comparisons of fossils with their living counterparts. Plant-bearing arthropod coprolites are oval to cylindrical in shape and can be as much as 1 mm long, although most are smaller. Those that have been analysed contain the remains of various plant parts (e.g. leaves, stems, spores, pollen) derived from a variety of land plants, including lycopods, ferns, gymnosperms, and angiosperms. The earliest plant-bearing arthropod coprolites occur in Upper Silurian and Lower Devonian strata and thereafter become increasingly common in younger formations.

The oldest clear indications of herbivory which can be linked with a particular group of arthropods are lesions on Early and Middle Devonian stems. These lesions are similar to those produced by modern piercing and sucking insects, but the oldest remains of such insects occur in Permian strata.

Some of the most abundant and credible evidence of

herbivorous arthropods is provided by feeding marks on leaves. These consist of relatively small excisions where a portion of the lamina has been removed from the margins or inner parts of the leaves. A rim of reaction tissue is present along the edges of the undamaged lamina of most of the damaged leaves, confirming that feeding occurred while the leaf was alive and still attached to the parent plant. In some specimens the veins adjacent to the excisions have been dislocated, and in rare instances the growth of the leaf appears to have been stunted by the grazing. The excisions indicate that many of the leaf-feeding strategies used by modern insects appeared during the Palaeozoic (Labandeira 1998). These strategies include marginal feeding (Fig. 4.1.16.1a,b,d), which first appeared in the Late Carboniferous; hole feeding (Fig. 4.1.16.1c); skeletonizing; and window feeding (Fig. 4.1.16.1d), which developed during the Permian. Evidence of leaf mining, a feeding strategy which also provides the herbivore with shelter, typically consists of narrow irregularly sinuous bands on the lamina of fossil leaves (Fig. 4.1.16.1a). Such structures are well documented in Paleocene and younger strata, and have also been infrequently described from fossil leaves as old as Late Carboniferous (Stephenson and Scott 1992).

Small borings excavated in both living and dead tissues are common in the geological record, beginning in the Carboniferous. Some of them contain coprolites similar in morphology to those of termites and confirm that these specialized insects were present in the Cretaceous, if not earlier (Boucot 1990). Most of the borings, particularly the older ones, are usually attributed to the activities of beetles.

It seems clear from the fossil evidence that phytophagous arthropods were present during the Devonian, or perhaps in the Late Silurian, and had developed a variety of feeding strategies by the Late Carboniferous, which they continue to use. This stasis in feeding strategies is remarkable because many groups of arthropods became extinct at the end of the Palaeozoic, yet the phytophagous arthropod fauna which replaced the early arthropod fauna continues to follow the same feeding strategies. Furthermore, land plants have faced increasing attack by phytophagous arthropods since the Carboniferous, a trend which has accelerated from the Cretaceous to the present day.

Herbivory in dinosaurs

Study of the teeth of dinosaurs indicates that many were herbivorous, but direct confirmation from gut contents is limited to a single example: the gut of a Cretaceous hadrosaur contained many leaves of the conifer *Cunninghamites elegans*, as well as twigs, seeds, and fruits of other land plants.

Although dinosaur coprolites might be expected in the geological record, only a few reasonable candidates have been reported. The most acceptable of these are from the Late Cretaceous of Montana. If correctly interpreted they illuminate three links in a food chain. The coprolites range in size up to about 34 cm in diameter and are composed mostly of angular fragments of conifer wood, up to about 3 cm long. They also contain burrows which appear to have been produced by dung beetles (not unexpected in an area occupied by herbivorous dinosaurs).

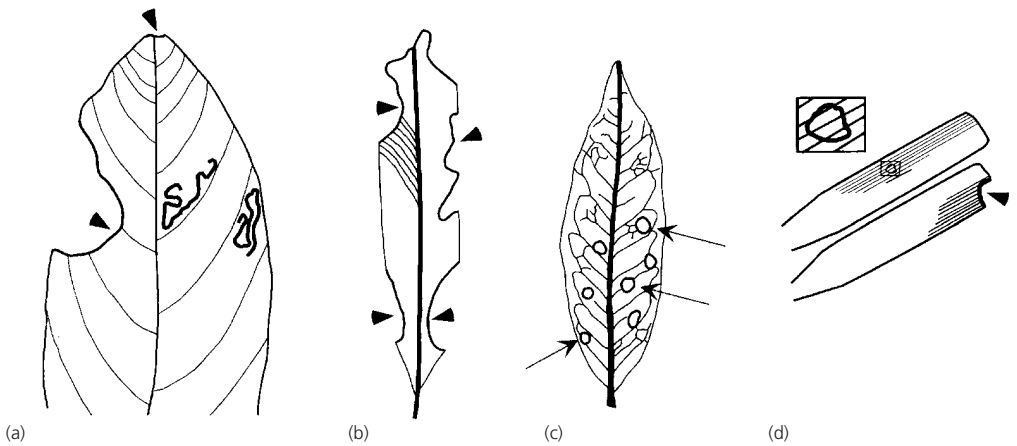

Fig. 4.1.16.1 Examples of feeding marks on fossil leaves. (a) Marginal feeding marks (arrowed) and leaf mines on an angiosperm leaf from the Eocene of Australia, ×0.5. (b) Marginal feeding marks (arrowed) on the leaf *Glossopteris* from the Permian of South Africa, ×0.5. (c) Hole-feeding marks (arrowed) on an angiosperm leaf from the Eocene of England, ×1. (d) Evidence of window and marginal feeding (arrowed) on two pinnae of the bennettitalean leaf *Zamites* from the Triassic of Utah, USA, ×1 (inset diagram ×10). (Adapted from Boucot *et al.* 1990; Stephenson and Scott 1992; fossils in the author's collection.)

Herbivory in mammals

Study of the teeth of mammals indicates that herbivory developed in this group early in the Cenozoic. The oldest direct evidence is the gut contents of horses and other ungulates from a Middle Eocene oil shale deposit near Messel, Germany (Schaal and Ziegler 1992). These confirmed that the horses were browsers, as deduced from earlier studies of their teeth, and that they inhabited a subtropical forest. Probably the most celebrated examples of gut contents are found in the carcasses of woolly mammoths, rhinos, horses, bison, and other mammals recovered from frozen Pleistocene silt and gravel deposits in Siberia and Alaska (Boucot *et al.* 1990). Analyses showed that they were dominantly grass-eaters, inhabiting a grass-covered, treeless plain.

Relatively few coprolites have been attributed with certainty to specific mammal taxa. Most of these occur in caves and rock shelters and were produced by a limited range of mammals, including sloths, mammoths, and humans. Coprolites of sloths that once lived in the western USA during the late Cenozoic indicate that they fed on xeric plants, principally *Yucca* and *Agave*, and that the region was biogeographically very similar to that of today. In contrast, mammoth coprolites from the same general area indicate that they fed primarily on grass and sedge, now found living 1200 m higher up in the adjacent highlands (Mead *et al.* 1986). Study of human coprolites has been helpful in determining not only diet but also when and where certain plants were brought into cultivation.

References

Boucot, A.J. (1990) *Evolutionary paleobiology of behavior and coevolution*. Elsevier, Amsterdam.

Labandeira, C.C. (1998) Early history of arthropod and vascular plant associations. *Annual Review of Earth and Planetary Sciences* **26**, 329–377.

Mead, J.I., Agenbroad, L.D., Davis, O.K. and Martin, P.S. (1986) Dung of *Mammuthus* in the arid Southwest, North America. *Quaternary Research* **25**, 121–127.

Schaal, S. and Ziegler, W. (1992) *Messel*. Clarendon Press, Oxford.

Stephenson, J. and Scott, A.C. (1992) The geologic history of insect-related plant damage. *Terra Nova* **4**, 542–552.

Taylor, T.N. and Taylor, E.L. (1993) *The biology and evolution of fossil plants*. Prentice Hall, Englewood Cliffs.

4.1.17 Plant–Animal Interactions: Insect Pollination

W.L. CREPET

Introduction

Plants and their pollinators constitute a set of mutualistic relationships of great visibility, scale, economic importance, and ecological significance. Insect pollination also has potential evolutionary significance; for example, it is considered more energetically efficient than wind pollination, and pollination by highly faithful pollinators provides a mechanism for increasing the rate of plant speciation. Insect pollination is associated predominantly with the flowering plants, and most pollinators belong to the four orders of anthophilous (flower loving) insects: Coleoptera, Diptera, Lepidoptera, and Hymenoptera. The fossil record indicates that insect pollination preceded the advent of modern anthophilous insects (Labandeira 1998). Evidence for the evolutionary pattern of plant–pollinator relationships includes well-preserved reproductive structures of various clades of vascular plants; indirect fossil evidence of insect feeding behaviour, such as coprolites, gut contents, and insect damage; and a growing fossil record of relevant insect taxa (Grimaldi 1999). Exciting discoveries of fossil flowers also provide unprecedented insights into the history of plant–pollinator relationships among angiosperms (Crane *et al.* 1995; Crepet 1996). Patterns derived from these fossil data provide a framework for understanding the development of insect pollination in geological history.

Early plant–animal interactions

Plant–pollinator interactions have their origins in myriapods/insects feeding on spores, soon after the establishment of a terrestrial flora (sporivory; Labandeira 1998). Next came the transition from sporivory to pollen feeding (pollinivory), and then from pollinivory to insect pollination. These events were contemporary with the origin of seeds and involved morphological transformations that beg certain questions. In particular, what would attract a potential pollinator to both ovule-bearing and pollen-bearing organs during the establishment of these mutualistic relationships? Pollen is an obvious attractant/reward and source of nutrition, but what would attract possible pollinators to separate ovules? Possibilities include pollen droplets (sticky secretions, which are preserved in the seeds of certain Carboniferous pteridosperms; Taylor and Taylor 1993),

secretions of associated glands (Taylor and Taylor 1993), and nutritious ovular tissue (which today serves as a substrate for larval development in beetle-pollinated cycads). Another important question involves the origin of the bisexual reproductive structure that is typical of many anthophytes and, arguably, basal within the angiosperms. Did it evolve merely by the condensation of organs that were already part of an interconnected branching system in monoecious taxa? Or was it the result of a more complicated evolutionary process where selection affected development in such a way that both sexes were expressed proximally in order to maximize pollinator efficiency? The events prompting these questions played themselves out in the Carboniferous, Permian, and Mesozoic.

Upper Palaeozoic

In the Carboniferous, insect pollen-feeding is documented by hemipteroid and orthopteroid coprolites (Labandeira 1998); other evidence suggests that insect pollination was established within the pteridosperm lineage before the Permian (Labandeira 1998). For example, medullosan pteridosperm pollen organs were sometimes very large and complex (e.g. *Dolerotheca*); these are hard to explain in functional terms except as attractants (highly concentrated and presumably visible rewards) to pollinators. The pollen itself was so large (often 600 µm in diameter) that effective wind dispersal seems most unlikely, especially in view of the patchy distribution of the taxa producing these pollen grains (Taylor and Taylor 1993). Cycads, the most primitive of extant seed plants, are generally considered to be closely related to pteridosperms. Modern cycads are pollinated by curculionid beetles, which appeared in the Mesozoic. Reports of Carboniferous cycads provide early evidence of insect pollination, and imply a historical shift in their pollinators. More fossil evidence is needed to clarify our understanding of modes and taxonomic distribution of putative insect pollination in the Carboniferous, and to evaluate the possibility that certain extinct insects (e.g. the Palaeodictyopteroidea) may have been important archaic pollinators (Grimaldi 1999). Ecological changes and a massive turnover in the flora and insect fauna at the end of the Palaeozoic would have terminated any previously established plant–pollinator relationships.

Mesozoic

The Mesozoic was a key period in the history of insect pollination. It included the origins of at least three new clades of insect-pollinated seed plants (Bennettitales, Gnetales, and angiosperms) and important radiations of anthophilous insects. Insect pollination in the early to mid Mesozoic may have been restricted to the 'cycadophytes' (cycads+Bennettitales), which were pollinated by Coleoptera (beetles). Extant Coleoptera demonstrate appropriate pollen and ovule feeding behaviour and were already diverse by the Mesozoic (Farrell 1998; Grimaldi 1999). The Bennettitales first appear in Triassic sediments and are currently considered part of the anthophytes (Bennettitales+Gnetales+angiosperms), despite their overt similarities to cycads. Newly interpreted data, however, reopen the possibility that they were related to the cycads. Thus, there may have been a single Palaeozoic origin of coleopteran pollination for the group cycads+Bennettitales. The pollination biology of early Bennettitales is too enigmatic to support this prospect, but there is considerable evidence of insect pollination in the Jurassic–Cretaceous bennettitalean genus *Cycadeoidea* (Taylor and Taylor 1993). This taxon had bisporangiate fructifications (analogues of the magnolialean angiosperm flower) that often preserve considerable insect damage, suggestive of pollen feeding by Coleoptera. Cone position and developmental sequence also mitigate against wind pollination.

Gnetales and angiosperms appear in younger Mesozoic deposits. The Gnetales experienced a major radiation at about the same time as the angiosperms (beginning at the base of the Cretaceous) and often co-occur with them. While species in at least two extant genera of Gnetales (*Ephedra* and *Gnetum*) are visited by nectar-feeding moths, there is no fossil evidence for the mode of pollination in early Gnetales. The distribution of insect pollination in the anthophytes raises the possibility that the flowering plants were originally insect-pollinated (if that character is a synapomorphy for anthophytes and not a parallelism that developed independently within the separate clades of anthophytes). Patterns of evolution in anthophilous insects are consistent with the appearances of Gnetales and angiosperms in the uppermost Jurassic–Lower Cretaceous. Significant families of pollinating Diptera, Acroceridae, and Bombyliidae are present by Upper Jurassic times, but anthophilic adaptations in these taxa do not appear until the Cenozoic (Grimaldi 1999) and the fossil record suggests a Cretaceous–Tertiary radiation of Syrphidae ('flower flies'). Upper Jurassic nemestrinid flies imply flower-feeding, even if conservatively interpreted, suggesting a significance for Diptera as well as the already diverse Coleoptera in early angiosperm evolution. Some carefully interpreted fossil evidence suggests that the Lepidoptera began radiating no earlier than the base of the Cretaceous (Grimaldi 1999). In the aculeate Hymenoptera, Sphecidae appear in the Jurassic, vespids in the Lower Cretaceous, masarine wasps in the mid and Upper Cretaceous, and Apidae in the Upper Cretaceous (Grimaldi 1999).

Flowering plants

The relationship between insect pollinators and the flowering plants transcends in scope, ecological importance, and evolutionary significance all other plant–pollinator relationships. The success of the flowering plants (see Section 1.4.2), and the possible involvement of insect pollination in their attainment of overwhelming dominance among vascular plant species, has provoked a great deal of discussion. At issue are the relative ecological/evolutionary advantages conferred on angiosperms by attributes other than insect pollination. These include animal fruit dispersal (and its possible role in allopatric speciation), rapid generation time, advantages associated with the herbaceous habit, and the occurrence of favourable climatic conditions during a key time in angiosperm radiation (Crane *et al.* 1995; Crepet 1996).

The crux of the question involves whether taxa of significant insect pollinators evolved in concert with the angiosperms or whether they preceded them in the fossil record. The latter possibility implies that pollinators are not causally related to the massively successful diversification of the flowering plants. The conclusion that there was a decoupling of angiosperm and anthophilous insect radiations has been criticized, based on the taxonomic level used in the analytical approach, the conflation of the fossil records of Hymenoptera vs. Apidae, and the standards for accepting the validity of key fossil evidence. Analysis at the family level masks diversification of species (the actual biological entities) (Crepet 1996; Grimaldi 1999), and the misleading nature of this approach has been dramatically illustrated by a recent contradictory analysis of coleopteran radiation (Farrell 1998). With respect to bees (Apidae), the decoupling of any bee–angiosperm radiation is based on an initial appearance of the order Hymenoptera that includes many non-pollinating and non-specialized pollinators as well as the bees. Finally, the fossil evidence supporting early radiations of certain anthophilous insects has been called into question (Grimaldi 1999).

Flower fossils

Remarkable data on specific fossil floral structures (see Section 1.4.2), affinities and associated anthophilous insects (Crane *et al.* 1995; Crepet 1996; Grimaldi 1999) provide vital new evidence on the radiation of anthophilous insects and angiosperms. A pattern is beginning to emerge, involving two broad but distinct early phases in the evolution of insect pollination. 'Phase I' begins at the Jurassic–Cretaceous boundary and includes the Albian. It is characterized by a radiation of monosulcate pollen-bearing angiosperms and by the establishment of the basal tricolpate lineage; included is fossil evidence of lauralean flowers with inferior ovaries, chloranthoid pollen, and *Ceratophyllum*-like fruits (Crane *et al.* 1995). Magnolialeans and Winteraceae, embodying characters traditionally favoured in model 'primitive' angiosperms, are represented by leaves and pollen, but not by definitive reproductive remains. Floral and fruit remains of Lauraceae, Calycanthaceae, fruits compatible with Magnoliaceae, and flowers of basal Hamamelididae apparently adapted for insect pollination are found in younger 'Phase I' deposits. This array of early angiosperm flowers suggests that pollinators were predominantly generalists, like beetles, various flies, mandibulate or short-tongued moths, and sphecid wasps. The remarkable diversity of Diptera from the Lower Cretaceous suggests that they were more important than previously supposed during this early phase of the angiosperm radiation (Grimaldi 1999).

'Phase II' begins with the Cenomanian and is most dramatically manifested in the Turonian where unprecedented angiosperm floral diversity has been discovered in the Raritan Formation of New Jersey, USA (Crepet 1996). These fossils provide evidence of remarkable magnoliid floral diversity and include other examples of basal angiosperms. However, the deposits are most notable for the diversity of rosid/dillenid and asterid floral remains, and for the array of highly derived floral characters now associated with derived insect pollinators (Crepet 1996). The appearance of these characters and of unexpectedly modern taxa (e.g. Capparales, Ericales, Clusiaceae) now also associated with highly derived pollinators (particularly bees) suggests that a major radiation of higher angiosperms (the 'eudicotyledons') took place at the same time as major radiations in key derived pollinators (including Apidae). This possibility is supported by the occurrence of even more derived floral morphologies in slightly younger deposits. Further modernization of derived pollinators and floral morphologies occurred late in the Cretaceous and early in the Tertiary. More fossil evidence from the Upper Cretaceous may help to determine whether the identification of a third phase in angiosperm–pollinator relationships is warranted.

References

Crane, P.R., Friis, E.M. and Pedersen, K.R. (1995) The origin and early diversification of angiosperms. *Nature* **374**, 27–33.

Crepet, W.L. (1996) Timing in the evolution of derived floral characters: Upper Cretaceous (Turonian) taxa with tricolpate and tricolpate-derived pollen. *Review of Palaeobotany and Palynology* **90**, 339–359.

Farrell, B.D. (1998) 'Inordinate fondness' explained: why there are so many beetles. *Science* **281**, 555–559.

Grimaldi, D. (1999) The co-radiations of pollinating insects and angiosperms in the Cretaceous. *Annals of the Missouri Botanical Garden* **86**, 373–406.

Labandeira, C.C. (1998) How old is the flower and the fly? *Science* **280**, 57–58.
Taylor, T.N. and Taylor, E.L. (1993) *The biology and evolution of fossil plants*. Prentice Hall, Englewood Cliffs, New Jersey.

4.1.18 Plant–Animal Interactions: Dispersal

J.J. HOOKER and M.E. COLLINSON

Introduction

Dispersal of plant material by animals is a fundamental interaction in modern and ancient ecosystems. Biodiversity is maintained or increased as plants provide life-saving keystone food resources and animal dispersal enables plants to sample a wide variety of life-sustaining niches. The deposition of phytophagous and detritus-feeding arthropod faeces is one step in the complex recycling of organic carbon via decomposition and soil formation. These interactions are demonstrated even in the earliest terrestrial assemblages by coprolites, fossil gut-contents, arthropod mouthparts, and damaged plants (Chaloner *et al.* 1991; Collinson 1999).

The dispersal of plants to new growth sites enables survival and expansion of plant species, communities, and vegetation. Pleistocene mammalian megaherbivore extinctions may have resulted in a drastic reduction of seedlings due to loss of dispersal agents (Murray 1986). Dispersal involves a plant disseminule (=propagule or diaspore) such as a seed (e.g. pteridosperms, cycads, conifers, flowering plants) or a spore (e.g. ferns, lycopods) which carries the genetic material to produce a new plant. The seed contains an embryo plant whilst the spore germinates to form a gametophyte plant on which fertilization results in embryo production. Megaspores act as disseminules if they carry microspores (Kurmann and Hemsley 1999). The dispersal of seeds by animals (zoochory), in the past as well as today, involves coadaptation and diffuse coevolution (Collinson and Hooker *in* Chaloner *et al.* 1991). It is often the plant's way of turning seed loss by predation to its own advantage. Thus, by using an animal to move seeds away from competition with itself and other established plants, the parent plant will improve the chances of survival of its offspring (Abrahamson 1989).

The oldest evidence for feeding on disseminules is from borings in Carboniferous seeds and megaspores (Chaloner *et al.* 1991), perhaps attributable to the stylet mouthparts of palaeodictyopteran insects, or through invasions by oribatid mites (see Collinson 1999). The dominant vertebrate plant-eaters of the Permian and Mesozoic appear to have eaten all plant parts, as evidenced by rare gut-contents (Murray 1986). This lack of selectivity is unlikely to have led to modern dispersal strategies, which probably evolved in the Cenozoic. Although some subaquatic dispersal takes place today (e.g. by fruit- and seed-eating freshwater characiform and siluriform fish, whose earliest records are Eocene and Cretaceous, respectively; Benton 1993), most examples are from subaerial and aerial environments, involving insects and tetrapods, mainly birds, mammals, and a few reptiles (Abrahamson 1989). Transport of the disseminule includes adhesion to the outside of the animal (epizoochory), burial, including scatterhoarding (inhumation), and passage through the alimentary tract (endozoochory).

Epizoochory

There is no association with seed-eating and no known benefit to the host. The plant benefits from very long distance dispersal and the animal's likely visitation of suitable habitats where the disseminule may fall off. The disseminule may have hooks, barbs, or a viscidly adhesive surface which can become attached to the animal as it brushes past.

Barbed and hooked spores are common in the Devonian (Fig. 4.1.18.1a) and may have facilitated arthropod dispersal (Kurmann and Hemsley 1999); modern echinate spores are transported by ants. Pollen has been found in the interstices of the ventral plates of *Arthropleura* (a giant Late Carboniferous myriapod), probably received as a dusting from the environment (see Chaloner *et al. in* Chaloner *et al.* 1991). Surfaces of early arthropods, including mites, collembolans, and trigonotarbids (and later, millipedes), might have trapped and transported spores but no direct evidence yet exists.

Logically the origin of fur should extend back at least to the time of the earliest mammals (Late Triassic). However, the oldest direct evidence of mammalian epizoochory is from Late Eocene Dominican amber, where mammalian hairs are entwined in the hooks of a fruit of the bamboo *Pharus*. Hooks and spines are exceptionally rare on fossil fruits and seeds but they do occur on tiny (2 mm) Cretaceous fruits similar to those of modern *Circaeaster*, and on late Palaeogene and Neogene aquatic plants such as *Trapa*. Alternatively, these might be anchoring modifications for establishment (Collinson *in* Kurmann and Hemsley 1999).

Inhumation (burial) by insects

Ants carry seeds to their nests where they may be buried in conditions suitable for germination. Special

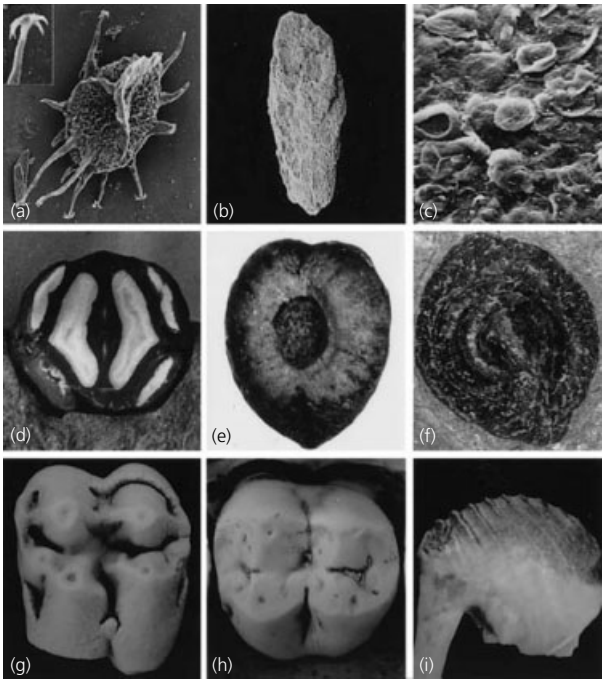

Fig. 4.1.18.1 Fossil evidence for dispersal. (a) Devonian spore *Hystricosporites* with hooked ornament (?for attachment to arthropods), ×75 (inset ×300). (b) Late Carboniferous coprolite, Yorkshire, England, ×10, containing (c) intact trilete spores, ×175. (d) Middle Eocene large nut of the walnut *Juglans* in TS, edible tissue in central ( )-shaped compartments; Clarno Nut Beds, Oregon, USA, ×1.5. (e) Early Eocene seed of *Parthenocissus* (Vitaceae, grapes), living relatives of which occur in fleshy fruits; London Clay, Sheppey, England, ×7. (f) Middle Eocene fleshy fruit (Menispermaceae) with outer skin, inner stone, and space between where flesh has decomposed; Messel, Germany, ×1.3. (g) Upper molar of the Eocene artiodactyl mammal *Acotherulum*; Bembridge Limestone, Isle of Wight, England, ×3; showing blunt cusps with worn tips characteristic of frugivores and like those of a modern dental analogue (h) the fruit-eating monkey *Cercocebus*; Recent, Cameroon, ×4. (i) Blade-shaped lower fourth premolar of the earliest Eocene multituberculate mammal *Ectypodus*, adapted for piercing dry seeds; Blackheath Beds, Abbey Wood, England, ×8. (a–c) Scanning electron micrographs; (d–i) reflected light micrographs. (a–c,f) Compressions; (e) permineralization with pyrite; (d) permineralization with silica. (a–c, Negatives loaned by A.C. Scott. Specimens in the following institutions: b,c, Hunterian Museum, Glasgow; d, Smithsonian, Washington, USA; f, Senckenberg Museum, Frankfurt, Germany; g–i, Natural History Museum, London.)

ant-attractant tissues (elaiosomes) adorn ant-dispersed seeds and inhibit seed predation (Abrahamson 1989). The oldest ants are Aptian (Benton 1993), postdating the earliest angiosperms by only a few million years. Many modern ant-dispersed seeds belong to dominantly herbaceous angiosperms with scant fossil record (Benton 1993). Even in the extensive legume fossil record, the Acacieae are few, and the important ant-dispersal syndrome in Australian *Acacia* probably evolved within the last 10 million years (Murray 1986). Seeds may be buried by dung beetles (Scarabaeidae) along with the dung. The oldest evidence of the scarabaeid dung-burying habit is Late Cretaceous (see Collinson 1999).

Scatterhoarding and 'nut'-feeding

Some rodents make caches (larderhoarding) whilst scatterhoarders (many rodents and some birds, e.g. corvids) bury seeds individually to prevent other animals from discovering the entire hoard. Dispersal will occur if the animal is unable to retrieve some of its hoard (e.g. through death) and the seed germinates.

Rodents have gnawing incisors which allow them to open hard dry fruits and seeds ('nuts') which are unavailable to most other frugivores and survive hoarding. The oldest known rodents are from the latest Paleocene of Asia and North America (Benton 1993), when angiosperm families that today produce rodent-dispersed nuts (Betulaceae, Fagaceae, Juglandaceae) were producing mainly smaller, often winged, nutlets (Collinson *in* Kurmann and Hemsley 1999). The larger nuts (Fig. 4.1.18.1d) became abundant in the Late Eocene, when rodents too underwent an explosive radiation. This coincides with the oldest evidence of rodent seed predation through gnawed openings in the aquatic monocotyledon *Stratiotes* (Collinson and Hooker *in* Chaloner *et al*. 1991).

The oldest records of larderhoarding are Miocene: a *Celtis*-filled kangaroo-rat burrow and an accumulation of *Carya* nuts in a tree stump (Collinson *in* Kurmann and Hemsley 1999), but direct evidence of ancient scatterhoarding is probably unobtainable. The oldest record of Corvidae is Miocene, before which time passerines as a whole are virtually unknown. Their involvement in scatterhoarding dispersal is thus likely to have considerably postdated that of rodents.

Endozoochory—spores

Gut-contents show that ancient arthropods fed on spores; coprolites containing spores show that they passed through the gut intact; and feeding experiments with modern arthropods show that spores are viable in faeces. Palaeozoic arthropod gut-contents containing spores are few, but intact spores in coprolites (Fig. 4.1.18.1b,c) are abundant in association with the earliest terrestrial assemblages (Silurian and Devonian) and amongst the coal-swamp floras of the Carboniferous (Chaloner *et al*. 1991; Collinson 1999). Feeding experiments showed that at least 6% of ingested bracken spores were viable in locust and giant millipede drop-

pings (Chaloner *et al.* 1991). It thus seems inescapable that arthropod dispersal of spores has occurred ever since the two invaded the land. Detritivory was a major arthropod feeding strategy at this time, although spore-feeding, piercing, and sucking did exist (see Collinson 1999). Arthropods feeding on detritus inevitably ingest spores from litter and hence potentially disperse them.

Endozoochory—seeds

The production by angiosperms of fleshy fruits (Fig. 4.1.18.1e,f) is aimed at potential mammalian and avian dispersers. The flesh, usually on the outside, is to provide the potential seed predator with an alternative food source. The seed embryo and its food reserve are often protected from digestion by a hard inner 'stone'. This may be smooth and ovoid to make it swallowable. Fleshy fruits vary in their nutritional value; more lipid- and protein-rich ones are preferred by birds, more sugar- and starch-rich ones by mammals (Murray 1986).

Fossil fruits and seeds whose nearest living relatives are fleshy and bird-dispersed are abundant in Middle Eocene and later floras (Chaloner *et al.* 1991; Kurmann and Hemsley 1999). However, most birds that feed on fleshy fruits today belong to families of the order Passeriformes (song birds), whose earliest undisputed records are Neogene (Benton 1993). The non-passerine frugivorous pigeons, hornbills, and toucans are no older, but other families occur in the Oligocene (trogons, cassowaries) or Eocene (pheasants, touracos, colies, oilbirds). Piciform birds with gut-contents containing seeds occur in the Middle Eocene of Messel. All these may have dispersed Eocene fleshy fruits.

The fossil record of mammals is good, and their most frequently preserved parts (teeth) are highly informative regarding ancient diets. Feeding on fruits or seeds requires pulping or crushing and the masticatory action involved (puncture-crushing) is produced by a vertical jaw motion. Modern fruit-eating mammals emphasize this action over shearing and grinding, which involves a more horizontal motion. Thus a typical mammalian cheek tooth adapted for frugivory has blunt cusps, little cresting, and wear is concentrated on the cusp tips (Fig. 4.1.18.1g,h). This morphology transgresses taxonomy, making it an important palaeoecological tool.

In the Mesozoic, most mammals had sharply cuspate and crested cheek teeth indicative of an insectivorous diet. However, the Late Triassic haramiyids and the later multituberculates and docodonts had blunt-cusped molars and must have included fruits or seeds in their diets. In the Paleocene, rapid radiation produced many placental frugivores to accompany the multituberculates. Most had enlarged piercing or crushing premolars (Fig. 4.1.18.1i), interpreted in multituberculates to be for the initial processing of dry seeds (analogous to the modern mountain pygmy possum *Burramys,* which has similar premolars). The plesiadapiform family Carpolestidae had similar adaptations, whilst the larger periptychids (primitive ungulates), in addition to having large conical premolars, display microwear consistent with feeding on hard dry fruits or seeds; the only Paleocene candidates for fleshy frugivory are picrodontid plesiadapiforms (Chaloner *et al.* 1991).

The near extinction of these groups at the end of the Paleocene was accompanied by the first appearance of modern orders, such as primates, artiodactyls, and bats, which contain most of the mammals that today consume fleshy fruits. The first primates were mainly insectivorous, but by the Middle Eocene there were numerous frugivorous types. Frugivorous artiodactyls diversified early, whereas frugivorous bats are virtually unknown until the Miocene. Most of these mammals lack specialized puncturing premolars and may have fed more on fleshy than dry fruits.

Preserved gut-contents in the Middle Eocene of Messel support the frugivorous diets deduced from tooth structure in an artiodactyl (*Aumelasia*) and a perissodactyl (*Propalaeotherium*). Those from the latter include *Vitis* (grape) seeds, conclusively demonstrating the consumption of fleshy fruits (Collinson 1999).

Consistent with the mammalian evidence, most Cretaceous and Paleocene fruits are small and dry, with only a few drupes (stone fruits) probably with little leathery flesh. In contrast, fleshy fruits from many angiosperm families (Fig. 4.1.18.1e,f) are abundant in the Eocene and the dispersal interaction between fleshy fruits and mammals diversified in this epoch (Chaloner *et al.* 1991; Kurmann and Hemsley 1999).

References

Abrahamson, W.G., ed. (1989) *Plant–animal interactions*. McGraw-Hill, New York.

Benton, M.J., ed. (1993) *The Fossil Record 2*. Chapman and Hall, London.

Chaloner, W.G., Harper, J.L. and Lawton, J.H., eds. (1991) The evolutionary interaction of animals and plants. *Philosophical Transactions of the Royal Society of London B* **333**, 177–288.

Collinson, M.E. (1999) Plants and animal diets. In: T.P. Jones and N.P. Rowe, eds. *Fossil plants and spores: modern techniques*, pp. 316–319. Geological Society, London.

Kurmann, M. and Hemsley, A.R., eds. (1999) *The evolution of plant architecture*. Royal Botanic Gardens, Kew.

Murray, D.R., ed. (1986) *Seed dispersal*. Academic Press, Sydney.

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4.2 Ancient Communities

4.2.1 Ecological Changes through Geological Time

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Introduction

Trends in the history of life are typically recognized by changes in taxonomic diversity (e.g. Sepkoski 1981). However, since the publication of *Evolutionary paleoecology of the marine biosphere* (Valentine 1973), a variety of palaeoecological approaches have been used to examine or characterize large-scale temporal patterns of evolutionary palaeoecology, ranging in focus from Phanerozoic palaeoecological patterns and trends to the recognition of community-level studies (see Section 4.2.2). Workers have also documented temporal patterns for particular environments such as the Phanerozoic history of reefs, which has received considerable attention (see Section 1.3.3). Less common have been examinations of the distribution of biofabrics such as stromatolites, shell beds, and ichnofabrics (see Sections 3.3.1 and 3.3.7).

Large-scale palaeoecological studies have become a significant component of our understanding of the history of life on Earth. This is due to contributions from evolutionary palaeoecology, including the demonstration that many palaeoecological processes that occurred in the past may not be occurring today; the utility of palaeoecology in examining the dynamics of broad-scale radiations (see Section 1.3), mass extinctions, and recoveries (see Section 2.3.10); and the recognition of the importance of biogeochemical cycles (see Section 1.1.4). The documentation of ecological stability at a variety of scales (see Section 4.2.2) has also invigorated research into temporal palaeoecological patterns. Here, the focus is on the Phanerozoic marine setting (see Behrensmeyer *et al*. 1992 on the terrestrial realm; Knoll 1994 on the Proterozoic) because an abundant fossil record has allowed the documentation of several large-scale trends, using a variety of measures of ecological change. Methods for the measurement of large-scale palaeoecological changes include analysis of: (1) guilds and adaptive strategies (Bambachian megaguilds); (2) tiering; (3) palaeocommunity composition and structure; (4) palaeoenvironments of individual clades and communities; (5) biofabrics; (6) analysis of specific types of behaviour and modes of life; and (7) palaeoecological levels.

Studies of biogeographical and taphonomic patterns through time, as well as analyses of possible trends in marine nutrients, are also instructive for deducing large-scale palaeoecological trends.

Increases in ecospace utilization: tiering, adaptive strategies, and guilds

Marine invertebrates have utilized more and more ecospace through the Phanerozoic; such increases, in part, correspond with the appearance of each of the three successive Evolutionary Faunas (Sepkoski 1981). Bambach (1983) introduced 'adaptive strategies' as a means of evaluating palaeoecological changes through time (e.g. Fig. 4.2.1.1). These are defined by life position (e.g. mobile epifauna) and general feeding type, and they include, for example, categories such as epifaunal mobile suspension feeders and pelagic carnivores. Whereas many workers have utilized the term 'guild' for these categories, Bambach (1983) referred to guilds as smaller subgroups within these adaptive strategy categories. The term 'Bambachian megaguilds' has thus been proposed for the adaptive strategies identified by Bambach (Droser *et al*. 1997). In an analysis of both guilds and Bambachian megaguilds, Bambach (1983) demonstrated that for each succeeding Evolutionary Fauna, more Bambachian megaguilds were utilized. The Cambrian Evolutionary Fauna had a relatively low diversity of adaptive types; nine megaguilds were established. Fourteen megaguilds were filled by the Palaeozoic Evolutionary Fauna, and 20—essentially all that are possible—are utilized by the Modern Evolutionary Fauna. In addition, through the Phanerozoic, the number of taxa within each megaguild increased, as did within-habitat diversity (Bambach 1977). In the Cambrian, each megaguild generally included just one or two class-level taxa, whereas by the end of the Ordovician, as the Palaeozoic Fauna became established, seven or eight class-level taxa were represented, particularly in each epifaunal megaguild. Bambach additionally demonstrated that the number of guilds ('groups of species that share a common mode of life, physiological constraints, and limiting resources'; Bambach 1983) within a given community increased from one Evolutionary Fauna to the next.

Tiering is the height above or depths below the sediment–water interface at which animals live (see Section 4.1.4). Tiering strategies show a more compli-

		SUSPENSION	DEPOSIT	HERBIVORE	CARNIVORE
EPIFAUNAL	MOBILE	Bivalvia	Gastropoda **Monoplacophora** **Ostracoda** **Trilobita**	Echinoidea Gastropoda Malacostraca **Ostracoda** **Monoplacophora**	Cephalopoda Malacostraca Stelleroidea Merostomata
	ATTACHED LOW	Articulata Edrioasteroida Bivalvia Anthozoa Stenolaemata Sclerospongia **Inarticulata**			
	ATTACHED ERECT	Crinoidea Anthozoa Stenolaemata Demospongia Blastoidea Cystoidea Hexactinellida **Eocrinoidea**			
	RECLINING	Articulata Anthozoa Stelleroidea Cricoconarida **Hyolitha**			

		SUSPENSION	DEPOSIT	HERBIVORE	CARNIVORE
INFAUNAL	SHALLOW PASSIVE	Bivalvia Rostrochonchia			
	SHALLOW ACTIVE	Bivalvia **Inarticulata**	Bivalvia **Polychaeta** **Trilobita**		Merostomata **Polychaeta**
	DEEP PASSIVE				
	DEEP ACTIVE		Bivalvia		

Fig. 4.2.1.1 General adaptive benthic strategies (megaguilds) that are typical of the Cambrian Evolutionary Fauna (in **bold**) and the Ordovician elements of the Palaeozoic Evolutionary Fauna. The shaded boxes are not biologically practical. (After Bambach 1983.)

cated history but with an overall pattern of increased tiering complexity reflecting increased ecospace utilization through the Phanerozoic.

Large-scale faunal turnovers: Ecological Evolutionary Units

Changes in community structure can occur at various scales (see Section 4.2.2) and large-scale patterns of faunal turnover have been documented (Boucot 1983). Intervals of time during which marine communities maintain stable ecological structure are called Ecological Evolutionary Units (EEUs). Twelve EEUs, which are characterized by different community types and distribution patterns, were originally recognized and later revised to nine EEUs (Sheehan 1996). Most of the EEU boundaries correspond to extinction events, and those following mass extinctions begin with short periods of reorganization. The compositions of these EEUs are controlled by the Evolutionary Faunas. Within each Evolutionary Fauna in a given environmental setting, the EEUs have similar ecological structures. Thus EEUs can be viewed as subdivisions of the Evolutionary Faunas (Sheehan 1996).

Palaeoenvironmental changes through time

Ecological changes include not only those within habitats or broad environmental settings, but also patterns in the palaeoenvironmental distribution of clades and

communities during their evolutionary history (see Section 2.3.1). These patterns have two aspects: (1) origination onshore; and (2) migration offshore. Offshore migration can take the form of expansion (maintaining onshore occupation while migrating to deeper water settings) or retreat (only occurring in offshore settings) (Bottjer and Jablonski 1988) (see Section 2.3.1).

One implication of onshore–offshore patterns is that the retreat or migration of a given clade affects not only its ecology and environmental preference but can also result in a shift in dominants within a given community. For example, isocrinid crinoids originated in the Triassic in onshore environments (Bottjer and Jablonski 1988). In certain nearshore settings in the early Mesozoic, these crinoids were the ecological dominant, i.e. they were a common (if not most common) element and thus served as a key species. Retreat of these crinoids from shallow-water settings over geological time resulted in a significant shift in community structure in nearshore environments.

There is an environmental bias in the distribution of the early appearances of communities made up of the Palaeozoic and Modern Faunas (Sepkoski and Miller 1985). As the Palaeozoic Fauna became established in the Ordovician, there was a shift from trilobite-dominated to brachiopod-dominated communities in shallow marine settings. In deeper water communities, trilobites maintained their dominant role.

Biofabrics

Biofabrics include those sedimentary fabrics that result in large part from a biological source or process. These include: (1) constructional fabrics (reefs, stromatolites, thrombolites); (2) fabrics formed through the concentration of individual sedimentary particles that are biological in origin, through primarily depositional but also erosional (winnowing) processes (shell beds, oozes); and (3) ichnofabrics. Use of biofabrics has proved to be a powerful means of examining ecological questions that cannot be addressed through the standard analysis of taxonomic composition. There was an increase in the physical scale of shell beds through the Phanerozoic (Kidwell and Brenchley 1994). This expansion was driven by evolutionary and ecological changes among hard-part producers, rather than any extrinsic geological conditions. An increase in hard-part durability, as well as the increasing occupation of high-energy habitats favouring winnowing and physical processes, provide the most likely explanation (Kidwell and Brenchley 1994). These ecological patterns could not have been deduced solely from an analysis of taxonomic composition of communities.

Cambrian and Ordovician shell beds show an increase of shell bed thickness through the Cambrian and a significant shift in abundance, thickness, and taxonomic composition at the base of the Middle Ordovician; this major change reflects the time when the Palaeozoic Fauna became established. Ordovician ichnofabrics, however, reveal that a significant increase in ecospace in the infaunal habitat, as documented by an increase in depth and extent of bioturbation, occurred later in the Late Ordovician. There are no known skeletal organisms at this time capable of such extensive burrowing, suggesting that soft-bodied burrowers appeared some time after the initial Ordovician radiation of skeletonized animals.

Comparative evaluation of palaeoecological change: palaeoecological levels

One of the greatest difficulties in evaluating ecological change based on the fossil record is that, in contrast to changes in taxonomic diversity, it cannot be readily enumerated. Thus, it is difficult to measure ecological change or structure. However, there are scales of change, i.e. some changes are far more significant than others. This structuring provides a means to scale or rank palaeoecological changes. Using this as a basis, ecological changes can be categorized into four ranks termed 'palaeoecological levels' (Table 4.2.1.1) (Droser *et al.* 1997). These levels are neither hierarchical nor additive, but they are ordered. Palaeoecological levels draw on a variety of types of measures that describe palaeoecology and recognize changes.

First-level changes are of the greatest magnitude and represent the advent of a new ecosystem. These types of changes include the beginning of life on planets such as Earth and Mars, and on Earth the advent of metazoan life on land, the sea floor, the deep sea, and the pelagic realm. In many respects, these types of ecological breakthrough represent functional thresholds. Because they are at such a large scale and are unidirectional, first-level changes will seldom be considered in an analysis of trends through time.

Second-level changes occur within an established ecosystem, and represent major structural changes at the largest ecological scale (Droser *et al.* 1997). Structural changes include the first appearance of, or changes in, the dominant higher taxon within an ecosystem, such as the shift from trilobite- to brachiopod-dominated shallow soft-substrate communities in the Ordovician. Large-scale shifts in the nature of ecospace utilization are also included. Addition or reduction in the number of Bambachian megaguilds serves as a useful signal of second-level changes. The development or collapse of metazoan carbonate build-ups represents a major shift in the ecological structure of the marine ecosystem and is considered a second-level change.

Third-level changes include community-scale shifts

Table 4.2.1.1 Definition of palaeoecological levels and characteristic signals for each level.

Level	Definition	Signals
First	Appearance/disappearance of an ecosystem	Initial colonization of environment
Second	Structural changes within an ecosystem	First appearance of, or changes in, ecological dominants of high taxa Loss/appearance of metazoan reefs Appearance/disappearance of Bambachian megaguilds
Third	Community-type level changes within established ecological structure	Appearance and/or disappearance of community types Increase and/or decrease in tiering complexity 'Filling-in' or 'thinning' within Bambachian megaguilds
Fourth	Community-level changes	Appearance and/or disappearance of communities Taxonomic changes within a clade

within an established ecological structure, in particular the appearance or disappearance of community types (Droser *et al.* 1997). Within a community type, the filling-up of Bambachian megaguilds and an increase in tiering complexity would also constitute third-level changes. Fourth-level changes involve the appearance or disappearance of communities such as a succession of similar brachiopod communities. Fourth-level changes are common throughout the Phanerozoic and are similar in magnitude to most minor ecological changes.

These four palaeoecological levels provide a means to compare and rank ecological shifts associated with taxonomic events. Throughout the course of an event, there may be a series of ecological changes that can be recorded by palaeoecological levels. For example, third- and fourth-level changes may occur at various intervals throughout an event, but second-level changes may be concentrated at a specific interval. Additionally, it is well documented, particularly during extinction events, that taxonomic changes may be concentrated in a certain biogeographical region, such as the tropics or the poles, or may be stronger in the marine or terrestrial realm. Palaeoecological levels can be utilized to document the palaeoecological expression of these taxonomic patterns in a more rigorous comparative manner.

Early Palaeozoic radiations

The Precambrian–Cambrian radiation was the most significant event in the history of marine metazoans. First-, second-, third-, and fourth-level changes occurred through this time interval as metazoans became established in the sea (Droser *et al.* 1997). Clearly, a series of changes at several levels occurred as communities evolved from Ediacaran assemblages to 'small shellies' to typical members of the Cambrian Fauna. This radiation, regardless of its potential triggers or timing, was an ecological event, filling ecospace for the first time.

The Ordovician radiation (see also Section 1.3.1) provides an excellent opportunity to examine palaeoecological changes through a radiation because there is a continuous marine record of skeletal metazoans long before, during, and after the radiation. Palaeoecological changes associated with the Ordovician radiation of marine invertebrates include second-, third-, and fourth-level changes (Droser *et al.* 1997). However, evidence from both spores and trace fossils suggests that the initial radiation of life on to land occurred in the Ordovician. This constitutes a first-level change.

In the marine realm, second-level changes included a shift from trilobite- to brachiopod-dominated shallow shelf communities. This shift, clearly demonstrated from shell-bed analysis, signals the establishment of the Palaeozoic Evolutionary Fauna and its associated EEUs. Hardground communities shift from echinoderm- to bryozoan-dominated communities. Both of these changes resulted in the establishment of marine systems that persisted for most of the Palaeozoic. There are also new Bambachian megaguilds, including deep mobile burrows (Fig. 4.2.1.1). Stromatoporoid reefs appear for the first time during the Ordovician.

A major element of the Ordovician radiation was at the third level where, essentially, Bambachian megaguilds become 'filled' up to their Palaeozoic levels (Fig. 4.2.1.1; Bambach 1983). In the Cambrian many of the Bambachian megaguilds had one or two clades; whereas by the end of the Ordovician, several megaguilds had up to eight different clades. Additional third-level changes included increases in tiering complexity from two to four levels of epifaunal suspension feeders; in the shallow marine infaunal realm three tiers developed (see also Section 4.1.4). New community types also appear, including a receptaculites–macluritid high-energy nearshore community type, new orthid community types, and a bivalve–trilobite community type in offshore muds.

Abundant fourth-level changes, in the form of new

communities, accompanied these second- and third-level changes. This 'trickle down' effect is a consequence of the second- and third-level changes.

Palaeozoic extinctions

The Late Ordovician extinction was the second largest in the history of metazoan life (Sepkoski 1981). As much as 50% of all marine species became extinct. However, ecologically only third- and fourth-level changes occurred. Although reef communities were strongly affected by cool temperatures, the Silurian reefs that appeared soon after the extinction were composed mostly of the families of rugose and tabulate corals that had been present in the latest Ordovician reefs (Copper 1994). The Late Ordovician extinction was not a major event for the reef system as a whole. The changes included the loss of some dominant brachiopod groups and stromatoporoid sponges, but this is mirrored in the subsequent Silurian recovery by replacement with new groups of brachiopods and stromatoporoid sponges, representing third-level changes (Droser *et al.* 1997).

The Late Devonian extinction was closely similar to the Late Ordovician extinction in terms of taxonomic decline, with a loss of 21% of marine families, but was more significant ecologically than the Ordovician extinctions, with second-, third-, and fourth-level changes. Metazoan reefs were virtually destroyed. The areal extent of reefs shrank by a factor of 5000 from the Frasnian to the Famennian (Copper 1994). Reefs did not recover for the remainder of the Palaeozoic.

The pelagic Bambachian megaguilds were virtually vacated. Conodonts, graptolites, and cricoconarids were lost from the pelagic-suspension megaguild, and cephalopods, placoderms, merostomes, and chondrichthyans from the pelagic-carnivore megaguild. Graptolites had almost disappeared by the Emsian. In the pelagic-suspension megaguild, only three species of the dominant pelagic conodonts survived into the Famennian and, although squeezing through the bottleneck, all of the cricoconarids became extinct before the close of the first zone of the Famennian (Droser *et al.* 1997). The Bambachian epifaunal megaguilds experienced a major 'thinning', with the epifaunal-attached-suspension and epifaunal-carnivore megaguilds being hardest hit.

Thus, the Late Devonian and Late Ordovician represent an interesting palaeoecological comparison. Taxonomically, the Late Ordovician extinction was greater; however, it had no lasting impact, whereas the Late Devonian extinction made a profound impact.

End-Permian mass extinction and Triassic recovery

The end-Permian is the greatest of all Phanerozoic mass extinctions (e.g. Sepkoski 1981) (see Section 2.4.4). The aftermath of this mass extinction lasted throughout the Early Triassic (see Section 2.3.10). A variety of palaeoecological data from Lower Triassic marine strata can be used to assess this event in terms of palaeoecological levels.

Ecospace was to a large extent emptied by the end-Permian mass extinction (see Sections 2.3.10 and 2.4.4). Of the possible Bambachian megaguilds, only five are occupied in Early Triassic palaeocommunities documented from western North America, which are interpreted as typical of the Early Triassic worldwide (see Section 2.3.10). This is a significant drop from the 14 Bambachian megaguilds occupied during the Palaeozoic, indicating a very large second-level change (Droser *et al.* 1997). Other significant second-level changes due to this mass extinction include a major shift in ecological dominants for soft-substrate shelf communities, from brachiopod-dominated in the middle and late Palaeozoic, to bivalve-dominated in the post-Palaeozoic. Furthermore, in a similar second-level change, carbonate build-ups were also restructured during this extinction.

At the third level, one of the primary changes was a reduction in epifaunal tiering, from four epifaunal levels in the late Palaeozoic to typically one level in the earliest Triassic (see Section 2.3.10). Undoubtedly there were numerous fourth-level changes.

Mesozoic and Cenozoic changes

Numerous second-, third-, and fourth-level changes were associated with the Triassic recovery and the subsequent establishment of the Modern Fauna. Most striking was the addition of new faunas to 'refill' the Bambachian megaguilds and the establishment of scleractinian coral reefs. The end-Triassic and end-Cretaceous extinctions included many third- and fourth-level changes. Second-level changes associated with these extinctions are most dramatically pronounced in the terrestrial realm, as dinosaurs became dominant only to go extinct and ultimately be replaced by mammals. The documentation of the palaeoecological changes associated with these events represents a fruitful area of research.

References

Bambach, R.K. (1977) Species richness in marine benthic habitats through the Phanerozoic. *Paleobiology* **3**, 152–167.

Bambach, R.K. (1983) Ecospace utilization and guilds in marine

communities through the Phanerozoic. In: M.J.S. Tevesz and P.L. McCall, eds. *Biotic interactions in Recent and fossil benthic communities*, pp. 719–746. Plenum Press, New York.
Behrensmeyer, A.K., Damuth, J.D., DiMichele, W.A., Potts, R., Sues, H.D. and Wing, S.L., eds. (1992) *Terrestrial ecosystems through time: evolutionary paleoecology of terrestrial plants and animals*. University of Chicago Press, Chicago.
Bottjer, D.J. and Jablonski, D. (1988) Paleoenvironmental patterns in the history of post-Paleozoic benthic marine invertebrates. *Palaios* **3**, 540–560.
Boucot, A.J. (1983) Does evolution take place in an ecological vacuum? *Journal of Paleontology* **57**, 1–30.
Copper, P. (1994) Ancient reef ecosystem expansion and collapse. *Coral Reefs* **13**, 3–12.
Droser, M.L., Bottjer, D.J. and Sheehan, P.M. (1997) Evaluating the ecological architecture of major events in the history of marine invertebrate life. *Geology* **25**, 167–170.
Kidwell, S.M. and Brenchley, P.J. (1994) Patterns in bioclastic accumulation through the Phanerozoic: changes in input or in destruction. *Geology* **22**, 1139–1143.
Knoll, A.H. (1994) Neoproterozoic evolution and environmental change. In: S. Bengtson, ed. *Early life on Earth*, pp. 439–449. Nobel Symposium No. 84. Columbia University Press, New York.
Sepkoski, J.J. Jr (1981) A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology* **7**, 36–53.
Sepkoski, J.J. Jr and Miller, A.I. (1985) Evolutionary faunas and the distribution of Paleozoic benthic communities. In: J.W. Valentine, ed. *Phanerozoic diversity patterns*, pp. 181–190. Princeton University Press, Princeton, New Jersey.
Sheehan, P.M. (1996) A new look at Ecologic Evolutionary Units (EEUs). *Palaeogeography, Palaeoclimatology, Palaeoecology* **127**, 21–32.
Valentine, J.W. (1973) *Evolutionary paleoecology of the marine biosphere*. Prentice Hall, Englewood Cliffs, New Jersey.

4.2.2 Do Communities Evolve?

R.K. BAMBACH

Evolution and ecosystem change

Evolutionary change manifests itself in the fossil record at all scales of time and space (Parts 1 and 2 of this book document many of those evolutionary events and processes). As species change, community composition changes. New modes of utilization of ecospace appear when new higher taxa arise and diversify. Episodes of faunal turnover in the marine realm produce changes that break the Phanerozoic into intervals at different scales, each characterized by different biotic associations.

Community concepts range from the idea of the community as a superorganism to the view of the community as a random aggregation of populations in a local habitat. However, all community definitions are rooted in the fact that populations of a variety of species live together in local geographical areas. Whether or not these populations are tightly linked in coevolved structures, a variety of interactions (ranging from trophic activity to habitat modification) take place between these organisms, either contemporaneously or over time. The reality of coexistence and interaction justifies the recognition of community as a level in the ecological hierarchy and raises the possibility that communities might be sufficiently integrated to justify consideration of change in communities over time as an evolutionary process (see Ivany and Schopf 1996 for many viewpoints on patterns of community change; and for topics concerning evolutionary palaeobiology see Jablonski *et al.* 1996, which includes a detailed discussion by Bambach and Bennington on the question, 'do communities evolve').

In the marine realm the structure of ecosystems and interactions within them change with each faunal change (see Section 4.2.1). Various authors have labelled such patterns of change involving communities as community evolution, with genealogical or phylogenetic implications. Some have argued that communities might be related to each other by phylogenies, as species are, and diagrams with lines and merging patterns connecting different named assemblages of fossils have been published. However, when associations of particular genera are tracked with particular facies through time, communities appear to be environmental, not evolutionary, entities. Change, but not evolution of communities as units, is suggested in detailed descriptions of the changes in faunas in the Appalachian Basin (Brett and Baird 1995). In the transition from the Onondaga to the Hamilton fauna fewer than one-third of the Hamilton species are derived from lineages known earlier in the Appalachian Basin and about half of the new species seem to be immigrant taxa from other areas. Physical events, such as sea-level or climatic change, apparently provided the opportunity for evolution to occur while disrupted ecosystems restabilized, rather than evolution having been the trigger for the changes in these communities.

While some use the term community evolution and mean evolutionary connectivity akin to that in phylogenies of organisms, others use the term without any implied genealogical connectivity. The issue is whether the word 'evolution' is to be used as a noun incorporating a process system analogous to that understood for the evolution of species or just as a synonym for change without implying a regular process system involving variation, reproduction, heredity, and selection. Niles Eldredge (1985, 1989) described evolutionary theory as

the interaction of two hierarchies, the genealogical and the ecological (see Table 4.2.2.1). The genealogical hierarchy (genes, chromosomes, organisms, demes, species, monophyletic taxa) is a nested set of historical, spatiotemporally bounded entities with beginnings, histories, and terminations (Eldredge 1985). The 'glue', as Eldredge calls it, that gives the constituents of the genealogical hierarchy cohesion is 'more-making' (gene replication in mitosis and meiosis, reproduction, speciation, and evolutionary branching). The biological portion of the ecological hierarchy (molecules, cells, organisms, populations, communities, regional biotas) is a different functional system, dealing with 'matter–energy transfer', not information 'which is ensconced, at base, in the genome' (Eldredge 1985, p. 170). Do community-level entities evolve, as is the case for entities of the genealogical hierarchy, or do they simply change as their constituent genealogical entities (species populations) evolve?

Communities are not genealogical entities

New local communities develop in newly formed or recently vacated habitats by immigration, not by reproduction. The local populations inhabiting a new community are acquired from the species living anywhere with geographical access to the area occupied by the new community. This is the case from the recolonization of small mangrove islands by arthropods after experimental fumigation, to the return of flora and fauna to areas devastated by events such as the explosive eruption of Krakatau in 1883, to the migration of the biota into recently deglaciated regions or regions where climate change forces major change in the ecosystem. These examples are at different scales, but each includes the formation *de novo* of new local communities by immigration of the founding members of the species populations.

Table 4.2.2.1 The genealogical and ecological hierarchies compared. The only shared entity is the organism.

Genealogical hierarchy	Ecological hierarchy
Monophyletic taxa	Regional biotas
Species	Communities
Demes*	Populations (avatars)†
Organism	Organism
Chromosome	Cells
Gene	Molecules

*A deme is a reproducing population, i.e. only those organisms in a local population that contribute genes to future generations.
†An avatar is a local population of reproducing, pre-reproductive, and post-reproductive organisms using and competing for resources in a habitat.

Comparable examples in the marine realm range from the colonization of barren dredge spoil to the return of marine conditions as epeiric seas flooded formerly exposed continental platforms during high-stands of sea level.

Numerous species transported by man have invaded areas remote from their natural distribution, demonstrating that species may fit into more than one community without any need, or time, for evolutionary modification. In fact, single species usually are not limited to membership in just one community, but frequently occur in several. When subjected to environmental change, communities do not necessarily maintain coherence. Species tend to migrate to other habitats and fit in wherever environmental conditions (including the biota) are adequate for their survival when environments change. This is well documented by the glacial–interglacial shifts in the Quaternary. On land, mammals with entirely non-overlapping modern ranges are known to co-occur in intermingled Pleistocene palaeocommunities, and a complete separation of geographical range has occurred since the Pleistocene for several European freshwater and land snails with formerly overlapping ranges. Species occurrence in marine communities is well known to have varied individualistically as climatic conditions fluctuated through the Pleistocene (Valentine and Jablonski 1993).

Breaching biogeographical barriers is another way in which species distribution patterns may change and communities can be modified, yet with little evolution taking place. The formation of the Central American isthmus permitted migration of terrestrial mammals between the North and South American continents. Ground sloths ranged from South America up to North Carolina and North American mastodons reached central Chile and Argentina. The immigrant taxa came in and modified the make-up of local communities while many of the native mammals persisted in their original settings. A major marine interchange took place when the Bering Strait opened in the Pliocene, permitting exchange between the Pacific and the Arctic–Atlantic, but no species-level morphological divergence occurred in most invading genera. Yet these invading species entered into entirely new community contexts in the territory they invaded.

Communities are not unified individuals. It is clear that many species are not limited in their occurrence to single communities, and that community composition can change without much or any evolutionary response by the constituent species. Nor are communities precisely bounded entities, despite the presence of interactions between some constituent taxa. In many instances species are arrayed independently along environmental gradients and communities simply represent the overlapping distribution of organisms within segments of

these gradients. This has been repeatedly demonstrated by ordination techniques. Distribution along gradients is also the common situation for marine palaeocommunities, as demonstrated by many studies of Palaeozoic assemblages. In fact, the recognition of particular fossil communities normally can be done only by subdividing a continuum. In practice, palaeocommunities are arbitrarily designated, even when samples are grouped objectively by cluster or factor analysis. Depending on whether species abundances (quantity) or species composition (presence–absence) is emphasized, different groupings of samples may result when subdividing the same continuum. There are no unambiguous natural seams to cut in these cases.

Palaeocommunities would be identified ideally by grouping samples ecologically, but fossil assemblages are composed of time-averaged accumulations and, because of taphonomic losses, are incomplete samples of the biota at best. Time-averaging, which is a normal factor in forming fossil assemblages (see Section 3.2.7), prevents determination of contemporaneity among specimens and obscures the record of patchiness or of seasonal fluctuation of populations, or even the variation in presence of species on longer time scales. Therefore, it is not possible to construct meaningful groupings of fossil assemblages using criteria such as interaction. The full network of interactions in an ecosystem cannot be observed in the fossil record, and inferred reconstructions are always somewhat hypothetical because of both time-averaging and partial preservation.

Should change in ecosystems be regarded as evolution?

What about the criteria for evolution (variation, reproduction, heritability, and selection) as applied to communities? Communities vary, and so do the entities at higher levels of the ecological hierarchy, and this variation is observed at all time scales. But variation is only one criterion needed for the process of evolution to operate. Are communities also individuals capable of reproduction, do they have heritability, and are they capable of undergoing selection?

Species are not restricted to membership in single local communities, or even to membership in more encompassing community types. Also, community-related entities of all sorts are simply arrayed as arbitrarily designated portions of environmental gradients. Hence, communities do not have the requisite bounding conditions to be regarded as unified individuals. Even though interactions occur in local communities, those interactions alter as species membership changes, which occurs frequently. In most instances the interactive network is not a fixed system, and therefore communities cannot be regarded as internally unified individuals either. Community-related entities are not unified individuals and thus they are not capable of reproduction. If community-related entities are not unified individuals capable of reproduction, then community-related entities cannot be characterized by heritability. There is no heritability in communities, only in their constituent taxa. Selection cannot act on communities as units because community-related entities are not reproducing individuals with heritability. Therefore, community-related entities do not possess the requisite properties and characteristics to support a process comparable to the evolution of species.

But community-related entities do change over time. Changes in local communities arise from: (1) stochastic variation; (2) environmental change; (3) the immigration and emigration of taxa; (4) the evolution or extinction of species; (5) the adjustment in abundance caused by interactions after a taxonomic change; and (6) coevolutionary responses (such as character displacement) stimulated by change in one or more member species. Factors (1–3), and (5) are not evolutionary processes; only (4) and (6) are strictly evolutionary and they only affect a portion of the local community.

Evolution does occur within local communities, as happened in the Galapagos after the initial taxa had arrived from other places, and this does change community entities. Species also evolve in concert and in response to interactions between them (coevolution) and this is truly evolution within and as part of local communities. However, although coevolution may markedly change or integrate parts of local communities, it is evolution in only part of an ecological entity, not evolution by the entity as a whole. Conversely, many species persist unchanged through disruptions of old communities to regroup into new communities. It appears that change is a ubiquitous feature of the Earth's ecosystems as environments change through time, but one that does not always have a great impact on the tempo of evolution and extinction.

Both evolutionary and non-evolutionary events combine to produce changes at all levels of the ecological hierarchy. But evolution itself is a process restricted to the genealogical hierarchy. The genealogical and ecological hierarchies are 'worlds apart' (Eldredge 1985, p. 170). Eldredge goes on to say, 'it is at the blatantly cross-genealogical level of communities that the independence of these two process hierarchies becomes utterly clear and justifies the recognition of two separate hierarchies.' The reason for this is that 'more-making, the general process that provides the temporal cohesion for next larger genealogical entities, does not enter into consideration of cohesion of the elements of the ecological hierarchy' (Eldredge 1985, p. 168). 'If we restrict the term "evolution" basically to the fate of genetically based information, evolution is probably best thought of

strictly in connection with the genealogical hierarchy' (Eldredge 1989, p. 189). Community-related entities in the ecological hierarchy just change—they do not evolve.

References

Brett, C.E. and Baird, G.C. (1995) Coordinated stasis and evolutionary ecology of Silurian to Middle Devonian faunas in the Appalachian Basin. In: D.H. Erwin and R.L. Anstey, eds. *New approaches to speciation in the fossil record*, pp. 285–315. Columbia University Press, New York.

Eldredge, N. (1985) *Unfinished synthesis*. Oxford University Press, New York.

Eldredge, N. (1989) *Macroevolutionary dynamics*. McGraw-Hill, New York.

Ivany, L.C. and Schopf, K.M., eds. (1996) New perspectives on faunal stability in the fossil record. *Palaeogeography, Palaeoclimatology, Palaeoecology* **127**, v–viii, 1–361.

Jablonski, D., Erwin, D.H. and Lipps, J.H., eds. (1996) *Evolutionary paleobiology*. University of Chicago Press, Chicago, Illinois.

Valentine, J.W. and Jablonski, D. (1993) Fossil communities: compositional variation at many time scales. In: R.E. Ricklefs and D. Schluter, eds. *Species diversity in ecological communities*, pp. 341–349. University of Chicago Press, Chicago, Illinois.

4.2.3 Palaeobiogeography of Marine Communities

G.R. SHI

Introduction

Palaeobiogeography is concerned with the distribution of fossil biotas as individual taxa or natural communities in both space and time. It differs from historical biogeography and ecological biogeography by involving immense time and seeking to explain present-day distributions of fossil biotas in the context of changing palaeogeography and palaeoclimate. The spatial aspect of palaeobiogeography usually concentrates on specified geological time horizons and aims to identify geographical patterns of fossil distributions and to determine the controlling mechanisms. The historical aspect of palaeobiogeography, on the other hand, traces how world provincialism waxed and waned through time. In studies where comprehensive data on fossil distributions through a succession of geological times are available, a full-scale, three-dimensional analysis of time vs. space vs. communities/taxa can reveal the evolutionary dynamics of biotas in both space and time.

Biogeographical hierarchy and principal determinants

Just as the modern biosphere can be classified hierarchically, so too can fossil biotas. In this hierarchical system, three subdivisions are usually recognized: realm, region, and province. Subregions, subprovinces, and lower community ranks are also identifiable, although it is not always necessary for every rank in the hierarchy to be recognized. In this context, the realm is regarded as the first-order biogeographical unit distinguished on a global scale by the presence (or absence) of endemic orders, superfamilies, and/or families. Although in theory recognition of realms is not based on large-scale climatic zonation, studies of modern biogeography and palaeobiogeography have demonstrated a distinct correlation between major realms and major palaeoclimatic zones, suggesting that the primary control on large-scale global distributional patterns of organisms is latitude-related climate and hence temperature gradients.

Within each marine realm, areas of endemic or characteristic families, subfamilies, and genera may be recognized as regions. A biogeographical region may be characterized as a vast aquarium confined within the limits of one realm and barred from other aquaria by environmental determinants. In delineating and accounting for biogeographical regions, the role of geographical barriers must not be underestimated for they can be as significant as climatic zones. For shallow marine benthos, large land masses and deep oceans commonly form provincial and regional boundaries.

Regions may be divided into provinces, each defined as a spatially contiguous area inhabited by a characteristic association of genera and species and bounded by ecological determinants that restrict dispersal of species and genera to and from the area. At this level, the major ecological determinants may include temperature gradients, geographical barriers, and ocean currents, as well as locally important factors such as salinity. In palaeobiogeography provinces are usually and necessarily defined on the basis of genera and, less commonly, higher taxa, because of the immense time dimension and the incomplete fossil record, as opposed to the frequent utilization of species in erecting modern provinces. However, even modern provinces can be differentiated on generic records alone (Campbell and Valentine 1978).

Spatial aspects of palaeobiogeographical data and multivariate analysis

Two features are usually associated with palaeobiogeographical datasets: (1) the distributions of taxa or communities in a region are neither random nor uniform, but tend to form certain lumpings (disjunctions) or gradients; and (2) certain taxa tend to occur together (spatial concordance) and disassociate with others (spatial discordance), a property collectively known as spatial autocorrelation. To a large extent, recognition of these features dictates the selection of an appropriate method(s) for a palaeobiogeographical study. For instance, spatial lumping can be detected by cluster analysis and gradient patterns by ordination techniques.

Cluster analysis (CA) vs. ordination analysis (OA)

Both CA and OA belong to a group of multivariate statistical methods aimed at summarizing large datasets. In biogeography these methods are often regarded as phenetic approaches as opposed to phylogenetic methods. In both CA and OA, an initial data matrix is required for calculation, consisting of individual or composite fossil localities as 'samples' (operational geographical units, or OGUs) and taxa (species, genera, or higher taxa) as 'variables' (operational taxonomic units, or OTUs). In these methods, both OGUs and OTUs are viewed as points in space; therefore the term 'point pattern analysis' has also been advocated.

CA is a heuristic classification technique devised to recognize discrete groups within a dataset. It does not require the data to be multinormally distributed, nor variables to be linearly correlated with underlying environmental gradients, but assumes the existence of discrete groupings. This assumption appears realistic where many palaeobiogeographical datasets are characterized by patchiness or disjunctions. Because of this underlying assumption, CA always forces objects into groups, even if the data points are randomly distributed. Geometrically, CA may be regarded as a data manipulation strategy that provides an explicit graphic display (dendrogram) that links OGUs or OTUs hierarchically to one another depending on their mutual similarities and the linking techniques used. Mutual similarities between OGUs are calculated using similarity coefficients. The most appropriate binary similarity coefficient for multidimensional palaeobiogeography is the Jaccard coefficient (Shi 1993).

Ordination means ordering or arrangement of OGUs or OTUs so that their disposition may be related to some underlying biogeographical determinants by displaying the spatial variations of OGUs or OTUs in a two- or three-dimensional coordinate system. In this approach the structure of underlying environmental gradients and their relation to biotic variation in space are assumed to be unknown during the algorithmic manipulation of the data, and are inferred through interpretation of the ordination of OGUs or OTUs. Geometrically, ordination involves rotation and transformation of the original multidimensional coordinate system, and reduction of high dimensionality, so that major directions of variation within the original data can be more readily understood. In this treatment, no assumption is made about the existence of discrete groups in the data. Instead ordination assumes continuity, but still reveals grouping structure where it exists. In this regard, ordination appears to be a more general quantitative palaeobiogeographical method than CA. On the other hand, linear ordination methods (including polar ordination, principal component analysis, and principal coordinate analysis) do assume multinormal distribution of variables and a linear relationship between the variables and underlying environmental gradients. These prerequisites are seldom met by palaeobiogeographical data, which are usually heterogeneous owing to the large geographical scale and hence extremely 'long' environmental gradient(s) involved. This casts doubt over the applicability of the linear models to palaeobiogeographical analysis. However, if the aim of a study is purely descriptive, to summarize the original data and to reduce dimensionality, linear ordination models may still be useful. Non-linear indirect ordination models (detrended correspondence analysis and non-metric multidimensional scaling) do not assume a linear relationship between variables and underlying gradients, but instead implicitly attempt to fit the Gaussian response model to the data. These methods therefore are more appropriate for palaeobiogeographical data than linear ordination models.

Interpretation of palaeobiogeographical data

Interpretation of phenetic similarities

Values of phenetic similarities among OGUs may be interpreted either statically or dynamically. A static interpretation aims to reconstruct palaeogeographical features on a single geological time horizon. In contrast, a dynamic approach seeks to reconstruct a succession of events and processes through comparison of successive geological time slices. The most obvious static interpretation of phenetic similarities among OGUs relates the binary similarity values to palaeogeographical distances in an attempt to reconstruct the relative palaeogeographical positions of crustal plates. This approach is unique in providing an approximation of the palaeolongitudinal separation of crustal plates, complementing the palaeomagnetic approach to palaeogeographical reconstructions. For example, the decrease of

phenetic similarity between the Permian Brachiopoda of the Shan-Thai terrain in South-East Asia and those of Gondwana, mirrored by an increase of phenetic similarities with the Cathaysian blocks, is interpreted as a consequence of increasing palaeogeographical separation from northern Gondwana and convergence with Cathaysia (Fig. 4.2.3.1) (Shi and Archbold 1998).

In a dynamic interpretation of phenetic similarities among OGUs of the same or similar age, the phenetic similarity values are expressed as an area cladogram illustrating the time relationship of the OGUs. For example, the cladogram in Fig. 4.2.3.2 shows that areas B and C with a similarity of 0.3 are assumed to be most recently separated and, conversely, A and B with a lower biotic similarity of 0.1 are assumed to have been biogeographically distinct, hence presumably geographically separated, for a longer period of time. This kind of dynamic interpretation, based on a single time horizon, is similar to the method of parsimony analysis of endemicity (PAE) (Rosen and Smith 1988). PAE was developed as a historical biogeographical approach and based on shared presences (endemicities) which were treated analogously to synapomorphies in cladistic systematics.

Interpretation of dendrograms and ordination graphs

A usual palaeobiogeographical interpretation of a

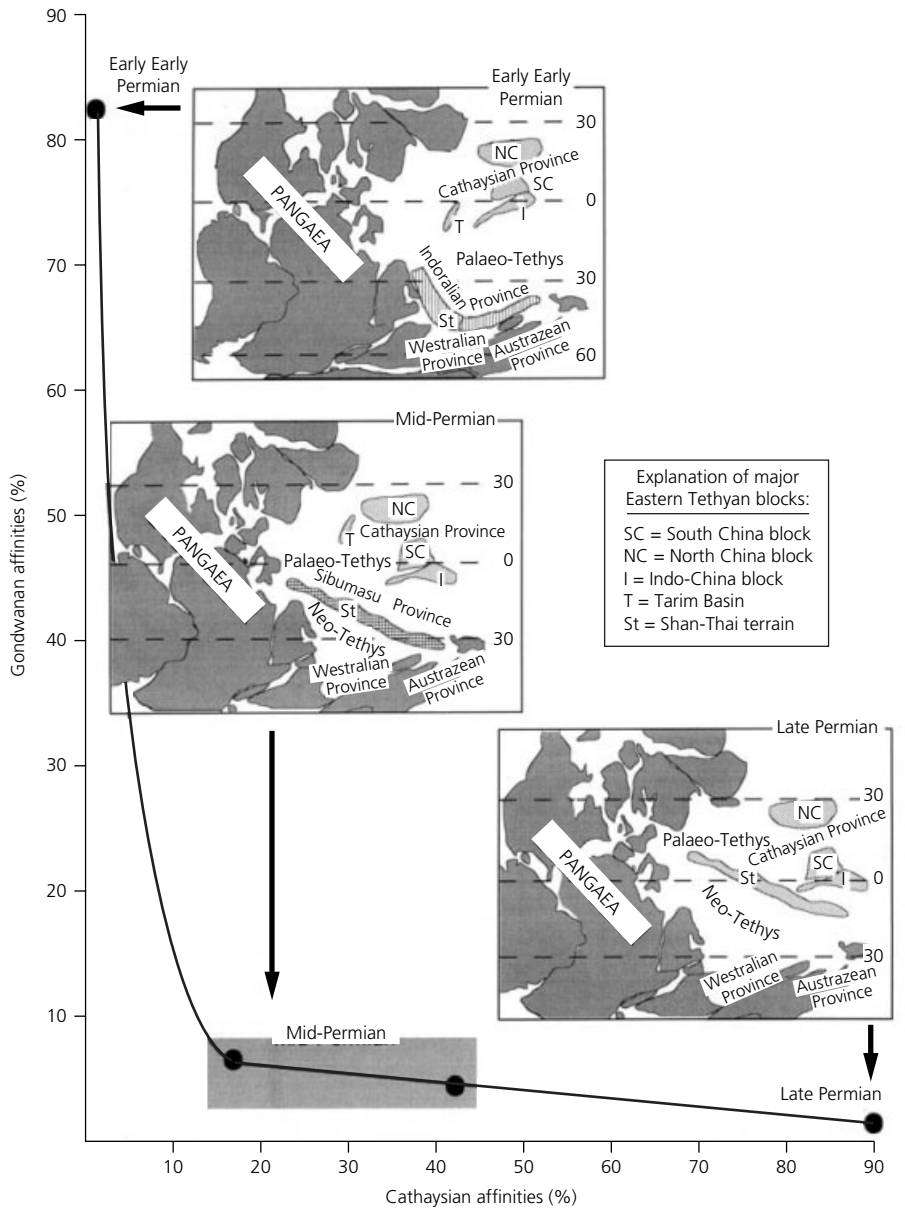

Fig. 4.2.3.1 An example of dynamic interpretation of phenetic similarities between coeval fossil biotas. During the early Early Permian, the Shan-Thai terrain demonstrates a high phenetic similarity with coeval Gondwanan brachiopod faunas, implying a close geographical proximity to Gondwana. However, as the Shan-Thai terrain advanced north, this similarity dropped rapidly at the beginning of the mid-Permian and then more gradually through the late mid-Permian and Late Permian, coupled with a concurrent, steady increase of Cathaysian affinity. This marked change of benthic marine provinciality through the Permian suggests that the Shan-Thai terrain was rafting to the north. At times during the Early Permian the dramatic turnover in provinciality was also enhanced by deglaciation, followed by a strong climatic amelioration. (See Shi and Archbold 1998 for details.)

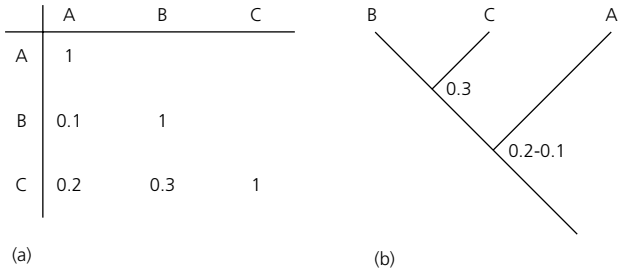

Fig. 4.2.3.2 A dynamic interpretation (b) of phenetic similarities (a) between OGUs A, B, and C. Areas with higher similarity values, B and C in this example, are assumed to be most recently separated and, conversely, areas with lower biotic similarities, A and B, are assumed to have been biogeographically distinct, and hence geographically separated, for a longer period of time.

dendrogram is to equate recognized clusters with biotic provinces. This single-tier interpretation recognizes that OGUs are spatially autocorrelated and groupings or patchiness can be found in nature. A dendrogram can also be interpreted hierarchically by viewing the dichotomies (nodes) of a dendrogram as equivalent to the hierarchical concepts of biotic provinces, regions, and realms (see Shi and Archbold 1993 for example).

The main purpose of all ordination methods is to reveal the environmental structure underlying a dataset, especially environmental gradients. This is achieved by relating the disposition of OGUs or OTUs in an ordination graph to some known or speculated biogeographical determinants. In practice, this may be undertaken by comparing the properties of data points at opposite ends of an axis to find the trend of the relevant properties. This trend can then be related or correlated to the variation of certain underlying biogeographical determinants (see Shi and Archbold 1995 for example).

Generating and testing palaeobiogeographical hypotheses

In 'neobiogeography', there exists two schools of thought as to how the present-day distribution patterns of biotas evolved: a 'dispersalist' and a vicariance approach. To palaeobiogeographers, the situation is further complicated by a plausible third interpretation: tectonic displacement. The applicability of these different interpretations to palaeobiogeographical data can be illustrated by a hypothetical example (Fig. 4.2.3.3). Assume that a modern disjunct distribution of a fauna has been identified. The two disjunct components of the fossil fauna are now separated by a vast geographical distance occupied by an ocean or land. The two components may be identical in taxonomic composition or slightly different, but not sufficiently different to suggest that they belong to separate biogeographical units. The three approaches mentioned above can be invoked to explain the origin of this disjunct distribution. From the dispersalist point of view (Fig. 4.2.3.3b), movement of elements of the fauna from point A to point A' is the result of long-distance dispersal across the ocean or land within a relatively short time geologically. In the vicariance model (Fig. 4.2.3.3c), however, the transportation of faunal elements from A to A' is seen as an effect of a tectonic event, which split part of fauna A away, and this fragmented continental area then drifted, carrying part of fauna A with it. In this interpretation, the occurrence of biotic evolution in the course of continental drifting is implied, but substantial similarities are still retained between A and A'. In terms of tectonic displacement (Fig. 4.2.3.3d), A and A' represent just one fauna, but some time after fossilization it was forcibly divided into different parts by a tectonic event. This interpretation is different from the vicariance approach in that the formation of fauna A' is considered to be a post-tectonic event, whereas in the vicariance approach the evolution and gradual formation of fauna A' is syntectonic.

Of course, the three interpretations are not mutually exclusive and a decision on which is correct may rely on other factors, such as time and geographical scale involved, and independent geological and geophysical evidence. Although the vicariance model has been increasingly favoured by historical biogeographers and the tectonic displacement approach by palaeobiogeographers, interpretations of phenetic similarities between OGUs have usually been based largely on the dispersalist model. The method that relates similarity values to palaeogeographical distance, for example, is based on the assumption that dispersal is the primary factor in controlling biotic distributions. Both linear and exponential models implicitly or explicitly use dispersal coefficients of specific faunal groups, which depend on both biotic and physical properties. Of course, the dispersal of a taxon is often complicated by tectonic events, and this requires the inclusion of this parameter in any mathematical model. Thus it is inappropriate to base a palaeobiogeographical interpretation on a single model; a balanced approach should be used, which assesses the validity and applicability of each model with respect to a particular case.

There are various ways of testing for the presence of spatial structure in palaeobiogeographical data, both quantitatively (statistically) and qualitatively. A hypothesis that provincialism at any particular geological time is related to palaeolatitude can be verified using the Mantel test of matrix correspondence. In this test, two matrices are calculated, one based on biotic dissimilarities of OGUs, the other on the actual palaeogeographical distances among the OGUs. The rationale underlying this test is to determine whether the biotic dissimilarities among the OGUs increase linearly with

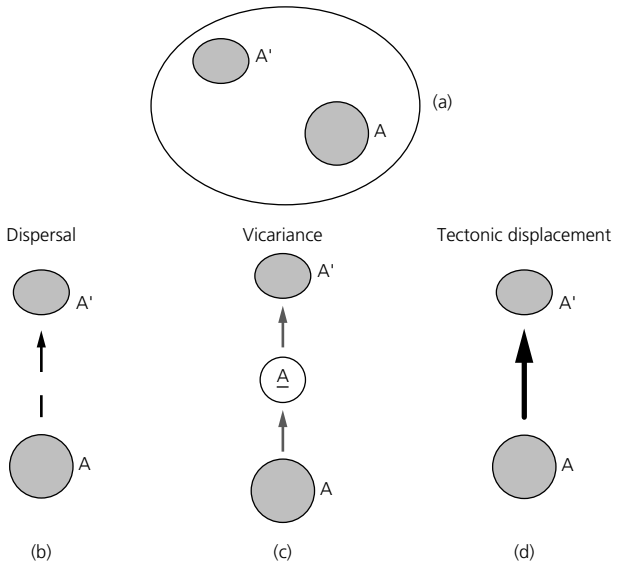

Fig. 4.2.3.3 Three plausible approaches (b, c, and d) to interpreting a disjunct distribution (a).

palaeogeographical distance. If this is the case, it means that a spatial gradient exists. However, this method is useful only if the relationship between biotic distributions and environmental variables is linear; it is not appropriate for multidimensional spatial structure, such as patchy patterns. In such cases, other quantitative tests must be used, including the Mantel correlagram technique and analysis of variance.

Palaeoclimatic, isotopic, and palaeomagnetic evidence provides qualitative tests of palaeobiogeographical interpretations. A common practice in palaeobiogeography is to estimate palaeolatitudes or palaeotemperatures on the basis of provincial structure and biotic diversity. One way of verifying these estimated palaeolatitudes or palaeotemperatures is to compare them with sedimentological data and quantitative values from oxygen isotopic and palaeomagnetic records.

References

Campbell, J.C. and Valentine, J.M. (1978) Comparability of modern and ancient marine provinces. *Paleobiology* **3**, 49–57.

Rosen, B.R. and Smith, A.B. (1988) Tectonics from fossils? Analysis of reef-coral and sea-urchin distribution from late Cretaceous to Recent, using a new method. In: M.G. Audley-Charles and A. Hallam, eds. *Gondwana and Tethys*, pp. 275–306. Geological Society of London Special Publication no. 37.

Shi, G.R. (1993) Multivariate data analysis in palaeoecology and palaeobiogeography—a review. *Palaeogeography, Palaeoclimatology, Palaeoecology* **105**, 199–234.

Shi, G.R. and Archbold, N.W. (1993) Distribution of Asselian–Tastubian (Early Permian) Circum-Pacific brachiopod faunas. *Memoir of the Association of Australasian Palaeontologists* **15**, 343–351.

Shi, G.R. and Archbold, N.W. (1995) A quantitative analysis on the distribution of Baigendzhinian–Early Kungurian (Early Permian) brachiopod faunas in the western Pacific region. *Journal of Southeast Asian Earth Sciences* **11** (3), 189–205.

Shi, G.R. and Archbold, N.W. (1998) Permian marine biogeography of SE Asia. In: R. Hall and J.D. Holloway, eds. *Biogeography and geological evolution of SE Asia*, pp. 57–72. Backhuys Publishers, Leiden, The Netherlands.

4.2.4 Deep-sea Communities

T. OJI

Introduction

Recognizing and reconstructing a fossil 'community' is difficult because of the limited evidence for ecological interactions between organisms. It is even more difficult for ancient deep-sea faunas, which are less abundant than those from shallow water. Therefore, the term 'community' is used here simply to denote a fossil assemblage that occurs at one or adjacent localities at the same stratigraphic horizon; the ecological interactions between organisms are not always considered.

What is 'deep sea'?

Marine environments are classified on the basis of ocean-floor topography: tidal, shelf, slope, floor, and trench. These subdivisions are also defined by water depth. In the biological or ecological sense, 'deep sea' ranges from 200 m to about 4000 m in depth; this corresponds to the continental slope, i.e. below the shelf edge and above the deep ocean floor. In the geological sense, 'deep sea' likewise corresponds to depths greater than 200 m, but is further subdivided into bathyal (200–≈2000 m), abyssal (≈2000–6000 m), and hadal (>6000 m). Precise depth estimation is virtually impossible on the basis of the fossil record, and terms such as 'upper slope' (upper bathyal) or 'deep ocean floor' (abyssal) are used in preference. Most of the deep-sea fossil record is bathyal (i.e. from the continental slope) but there are also examples of fossil communities thought to originate from the deep ocean floor.

Tropical and subtropical water is generally very clear. From the window of a submersible, very dim sunlight from above is detectable even at a depth of several

hundred metres. But nearshore, where the water is clouded by suspended matter, most sunlight is absorbed in less than 200 m. Primary production involves photosynthesis by plants and plankton living in the photic zone (except for chemosynthetic organisms in cold seeps and hydrothermal vents; see Section 4.2.5). Deep-sea organisms depend on the material that sinks down from these near-surface layers, i.e. fragments of small plants, photosynthetic plankton or animals, or the faecal pellets produced by animals. The number of individuals and the biomass of deep-sea communities is consequently much smaller than those on the shelf. This is evident in the oceans today, and must apply to deep-sea life in the geological past.

Criteria for deep-water environments

It is sometimes difficult to estimate the depth at which ancient sediments were deposited. The most reliable criteria are physical factors, which can be applied to a deposit of any age, rather than biological information about faunas characteristic of the deep sea today. Biological data can only be used to estimate bathymetry for late Tertiary or Quaternary sediments that yield a proportion of modern species or genera. This is because many marine animals are thought to have changed their bathymetric distribution through geological time.

Upper shelf sequences frequently contain storm deposits, and exhibit hummocky cross-stratification if the sea bed was above storm wave base. Such storm deposits are entirely absent from beds in the bathyal environment where, if anything, there are only turbidites and other enigmatic coarse sediments transported from shallow water by storm or submarine slides. Some fossil assemblages are the result of such transportation from relatively shallow water into a deeper setting (e.g. Burgess Shale fauna).

General characteristics of deep-sea communities

From a trawl or dredge of bathyal depths, the number of animals collected is usually smaller than from the continental shelf. Species diversity also decreases dramatically into deeper water. At a depth of a few hundred metres on the continental slope, only one or a few macrobenthic species are dominant. The decrease in species diversity at bathyal depths does not necessarily correlate with a decrease in numbers of individuals. Here the sea floor is often covered with concentrations of individuals of one or a few macrobenthic species only. For example, in the north-west Pacific, off the east coast of Japan, the ophiuroid *Ophiura sarsii* densely carpets the sea floor in the depth range 250–700 m (Fig. 4.2.4.1) (Fujita and Ohta 1990). Deep-sea photography shows that sea cucumbers are also very abundant at bathyal and abyssal depths.

Faunal composition also varies with depth. In Recent and Quaternary/Tertiary macroinvertebrate communities, bivalves and gastropods, among shelly fossils, generally dominate the shelf environment, together with smaller numbers of echinoderms. Deeper water, however, is the world of echinoderms (crinoids, asteroids, ophiuroids, echinoids, and holothurians). They are dominant, both in abundance and diversity, among invertebrates with a biomineralized skeleton. The shallowest record of a stalked crinoid is at 100 m, near the edge of the continental slope off southern Japan. Many crustaceans (especially copepods), cnidarians (e.g. sea pens, gorgonians, solitary corals), and siliceous sponges are also characteristic of the deep sea.

Example of a deep-sea community

The shallow-water deposits of epicontinental seas are widely distributed on all continents. In contrast, examples of deep-sea deposits and their fossils are restricted to tectonically active plate margins, such as Japan and western USA. In southern Japan, deep-sea fossils occur in many tectonically uplifted areas; even Pleistocene deep-water deposits are known. The Morozaki fauna is a remarkably preserved deep-sea fauna from the Early Miocene Morozaki Group, central Japan: it includes a variety of echinoderms, molluscs, crustaceans, and fishes (Tokai Fossil Society 1993). Although some elements of the fauna occur in turbidites (and were transported from shallow water to the deep sea), most of the fossils are of upper bathyal origin (several hundred metres deep). This Miocene Lagerstätte yields, among many others, brisingid asteroids, isocrinid crinoids, ophiuroids, echinothurioid echinoids, brachiopods, galatheid and gammarid crustaceans, and deep-water fishes (e.g. holosaurids, notacanthids, bathylagids, and many gonostomatids) (Fig. 4.2.4.2). The fossils usually occur in laminae just a few millimetres thick. Many are preserved intact, suggesting that they were buried rapidly (i.e. in an obrution deposit). Some of the deep-sea fishes preserve rows of luminous organs. Many taxa await further systematic work, but the fauna includes species or genera found today on the continental slope (several hundred metres to 1000 m deep) in the west Pacific and Indian oceans.

The deep sea as a refuge for 'living fossils'

It is well known that many kinds of 'living fossils' (extant organisms that have a long geological history without any conspicuous morphological change) are found in the deep sea. About 100 years ago, Alexander

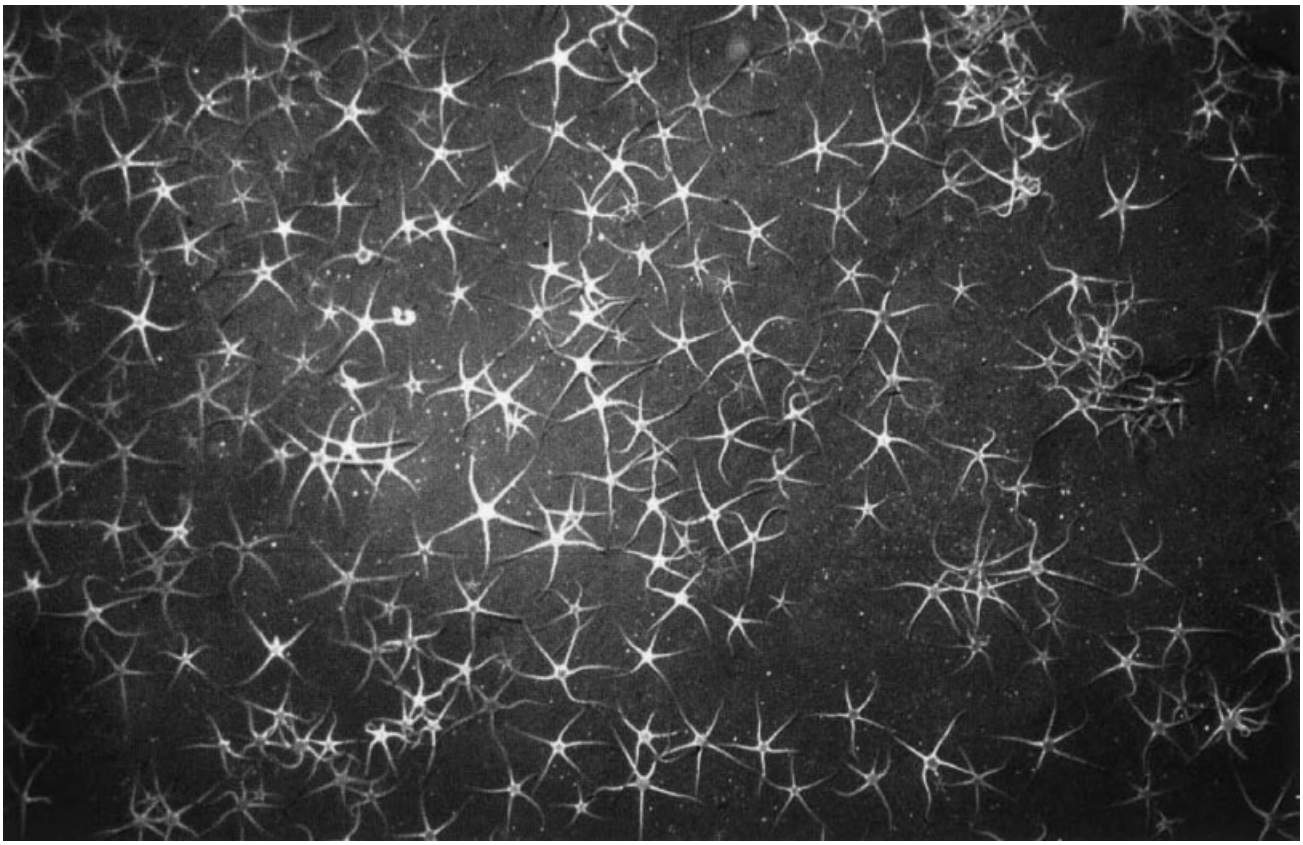

Fig. 4.2.4.1 Dense concentration of *Ophiura sarsii* on the upper continental slope (250 m deep) off north-east Japan. Individuals range in size from several centimetres to 10 cm across. (Photograph by T. Fujita, taken from the JAMSTEC submersible *Shinkai 2000*.)

Agassiz thought that many 'survivors of the former geological periods would be sure to be found' in the deep sea. Agassiz was wrong, in that most inhabitants of the deep sea resemble shallow-water forms, but none the less many living fossils are known only from the deep sea, e.g. the coelacanth *Latimeria chalumnae*, stalked crinoids, *Nautilus*, pleurotomariid gastropods, and the monoplacophoran mollusc *Neopilina sibogae*. Many of these living fossils have representatives in shallow-water deposits from the geological past.

Several marine benthic taxa have changed habitat, especially their bathymetric distribution, since the Palaeozoic (Bottjer and Jablonski 1988). These groups show 'offshore migration' or 'retreat from shallow water', i.e. they disappeared from shallow water sometime during the Mesozoic or Cenozoic. There are many possible explanations for this pattern, but biotic interactions (such as the impact of new bioturbators or predators) are the most plausible.

The most conspicuous feature of living fossils is their morphological conservatism. Other organisms adapt to a new environment by evolving new morphological or behavioural modifications (e.g. protective morphology, or infaunal life habit). Many living fossils, on the other hand, lack such adaptations, and have migrated from shallow to deep water. Stalked crinoids, for example, were a major constituent of shallow shelf communities until the mid-Cretaceous; since then they have been virtually restricted to deep water.

Similar habitat changes characterize various benthic communities; the retreat from shallow depths may have been linked to the 'Mesozoic marine revolution', i.e. increased predation by durophagous (shell-crushing) predators in shelf environments during the Mesozoic (see Sections 1.4.1 and 4.1.7). Observations on the stalked crinoid *Endoxocrinus parrae* from the western Atlantic suggest that shallow-water individuals are at a higher risk of non-lethal predation than deep-water forms (Oji 1996). The deep sea may be regarded as a safe haven for 'living fossils', unable to cope with the increased predation in shelf environments.

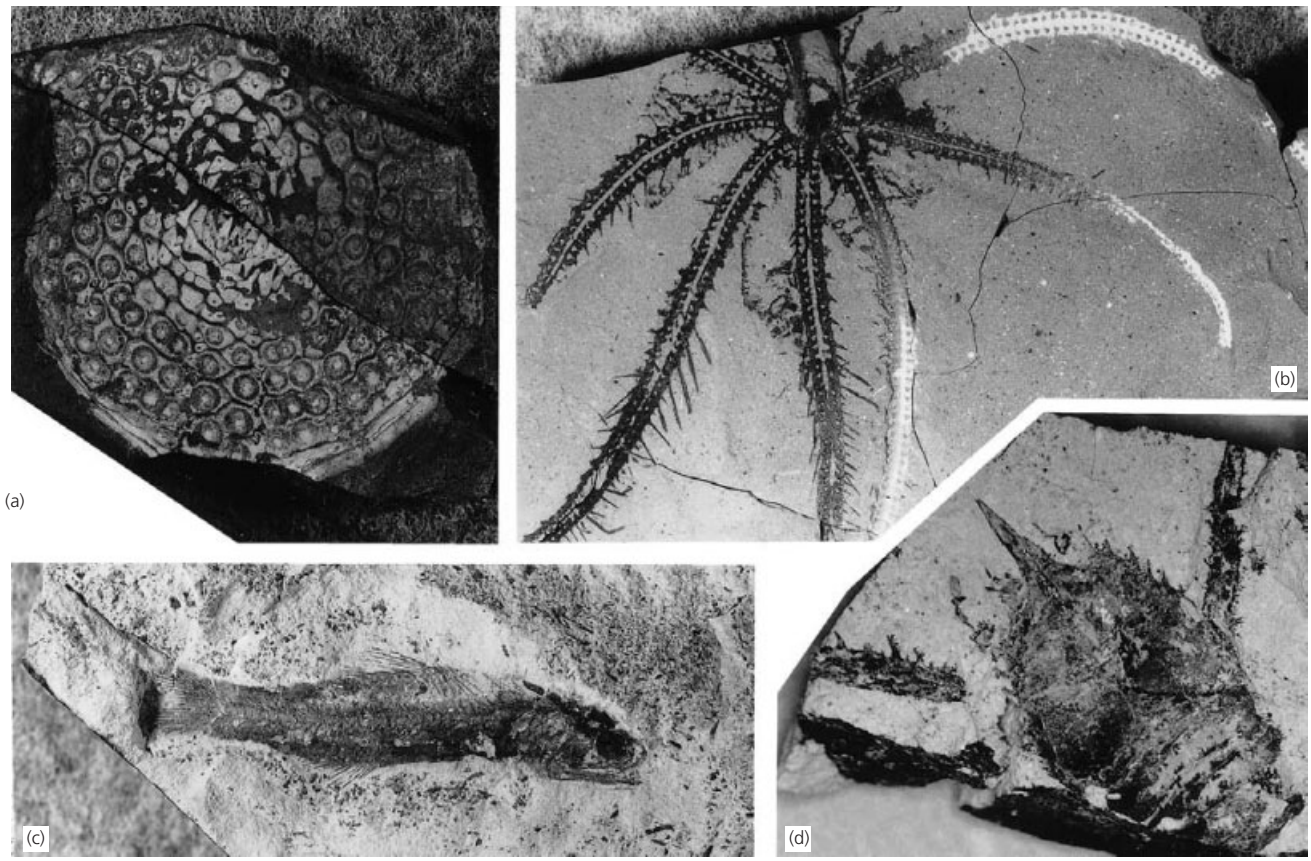

Fig. 4.2.4.2 Deep-sea fossils from the Early Miocene Morozaki Group, central Japan. (a) Echinothurioid echinoid *Phormosoma* sp., ×0.85. (b) Brisingid asteroid *Brisingella* sp., ×0.65. (c) Myctophid fish *Lampanyctus* sp., ×0.85. (d) Galatheid crustacean, ×1.55. (Photographs by K. Hachiya.)

References

Bottjer, D.J. and Jablonski, D. (1988) Paleoenvironmental patterns in the evolution of post-Paleozoic benthic marine invertebrates. *Palaios* **3**, 540–560.

Fujita, T. and Ohta, S. (1990) Size structure of dense populations of the brittle star *Ophiura sarsii* (Ophiuroidea: Echinodermata) in the bathyal zone around Japan. *Marine Ecology Progress Series* **64**, 113–122.

Oji, T. (1996) Is predation intensity reduced with increased depth? Evidence from the west Atlantic stalked crinoid *Endoxocrinus parrae* (Gervais) and implications for the Mesozoic marine revolution. *Paleobiology* **22**, 339–351.

Tokai Fossil Society (1993) *Fossils from the Miocene Morozaki Group*. Bisaisha, Nagoya. (In Japanese.)

4.2.5 Ancient Hydrothermal Vent and Cold Seep Faunas

C.T.S. LITTLE

Introduction

Modern hydrothermal vent and cold seep communities are unlike almost all other marine communities because: (1) they depend on geochemical rather than photosynthetic energy; and (2) their primary producers are chemosynthetic bacteria rather than photosynthetic plants. Hydrothermal vent and cold seep communities are found in places where geochemical energy sources—hydrogen sulphide and other reduced sulphur compounds in the case of vents, and these compounds and/or methane in the case of seeps—are issuing on to the sea floor.

Hydrothermal vents occur principally where new ocean crust is being formed at spreading centres on the mid-ocean ridges and in back-arc basins, but also on off-axis volcanoes. Modern hydrothermal vents are discontinuous in both space and time. They are often widely spaced along ridge axes and have episodic periods of activity, with total life spans of tens of years to tens of thousands of years. These dynamic factors have important implications for the animals that depend on a constant supply of hydrothermal fluid to exist.

Cold seep communities are found at passive continental plate margins in a variety of settings, including groundwater and hydrocarbon seeps and brine pools, and also at active plate margins in accretionary prisms. Subsurface carbonate deposits often form at seep sites and these have characteristic negative $\delta^{13}C$ isotope signatures (between about –30 and –50‰) which are a product of bacterial oxidation of methane generated by methanogenic bacterial metabolism and/or thermal processes. As far as is known, cold seep sites are more numerous than hydrothermal vents and individual seeps may exist for longer periods of time.

The animals that live at hydrothermal vents and cold seeps are remarkable for many reasons, not least for their physiological adaptations to these challenging environments. Hydrothermal vent and cold seep communities are dominated, both in terms of biomass and numbers of individuals, by animals with endosymbiotic sulphur- and methane-oxidizing bacteria. These relationships allow the animals to grow very quickly and appreciably larger than other deep-sea animals. A large number of vent and seep species are endemic (82% in the most recent analysis) and many are separated from their nearest relatives at high taxonomic levels (Tunnicliffe 1992). Based on these observations it has been suggested that some of these endemic species represent Mesozoic or even Palaeozoic 'relics', and that vents and seeps have acted as an extinction-resistant refuge.

At hydrothermal vent sites bacterial endosymbiotic relationships are formed by vestimentiferan tube worms, mytilid and vesicomyid bivalves (e.g. *Bathymodiolus* spp. and *Calyptogena* spp., respectively), and two species of provannid gastropod. Other important vent groups are the filter-feeding alvinellid polychaetes (some species of which live on black smoker chimneys, e.g. the 'Pompeii worm' *Alvinella*), grazing patelliform archaeogastropods, and scavenging/predatory bythograeid crabs and alvinocaridid shrimps. There are important biogeographical variations in the modern vent ecosystem; alvinellid polychaetes and vestimentiferans, for example, appear to be absent from the Atlantic vent sites.

Cold seep communities are similar in trophic structure to hydrothermal vent communities but can be more diverse and contain larger numbers of animal taxa that also inhabit neighbouring deep-sea habitats, such as hydroids, gorgonians, echinoderms, and brachiopods (Sibuet and Olu 1998). The group of cold seep animals with endosymbiotic bacteria includes not only vestimentiferans, vesicomyids, and *Bathymodiolus* spp., but also lucinid, thyasirid, and solemyid bivalves, and two demosponge genera.

Ancient hydrothermal vent communities from mid-ocean ridge and island arc related settings

The ancient analogues of the polymetallic deposits that form at modern hydrothermal vent sites are known as volcanogenic massive sulphides (VMS), and these deposits have significant economic importance, mainly for copper and zinc ore. They are found within volcanic rock sequences (representing former ocean crust) in ophiolites, accretionary prisms, and allochthonous terrains. Although more than 1000 VMS deposits are known, ranging in age from the Cenozoic to the Archaean, so far only 19 are known to contain hydrothermal vent fossils: one from the Eocene, one from the Paleocene or Late Cretaceous, seven from the Cretaceous, one from the Jurassic, six from the Devonian, and three from the Silurian (Little *et al.* 1998).

The fossil assemblages are preserved *in situ* in the upper parts of the VMS deposits and often occur with black smoker chimney fragments and colloform, fine-grained pyrite. All of the assemblages are dominated by clusters of worm tube fossils which are usually of small diameter (1–10 mm) and lack ornamentation. These have often been compared with sulphide-replaced tubes of modern vent alvinellid polychaetes and vestimentiferans but the lack of diagnostic characters on the fossil tubes makes a definitive identification difficult. Most of the fossil vent assemblages comprise tube worm fossils only, but a number also contain a small variety of molluscs and brachiopods. All the vent fossils are preserved as thin external moulds, showing details of periostracum, growth lines, and ornament, and sometimes also internal moulds. The majority of the fossil moulds are formed initially of thin layers of pyrite, often with colloform texture, but some of the worm tube walls are formed of framboidal pyrite. This early pyrite forms a template for the growth of variable thicknesses of laminated colloform pyrite, which may be microbial in origin. None of the fossil tube worms, brachiopods, and molluscs preserves any original organic tube wall/shell material, this presumably having been subject to rapid postmortem decay/dissolution.

The VMS deposits containing only small tube worms are found in ophiolites in the Philippines (Barlo deposit, Upper Eocene), New Caledonia (Azema deposit, Senonian or Paleocene), Oman (Bayda deposit, Cenomanian) and in the tectonic slices containing island arc

related volcanics which form the eastern slope of the middle and southern Ural Mountains of Russia: Uzelga (Middle Devonian), Yubileinoe, Buribuy, Safyanovka (all Lower Devonian), Krasnogvardeyski, and Ljeviha deposits (Silurian).

Other vent assemblages are more diverse. The Cenomanian age Troodos ophiolite of Cyprus contains a large number of VMS deposits and vent fossils have been found in six of these: Peristerka, Sha, Kapedhes, Memi, Kambia, and Kinousa. They all contain clusters of small, cylindrical, flanged worm tubes. Small specimens are loosely to tightly coiled (Fig. 4.2.5.1g,h); larger ones are straighter. They display an external ornament of concentric growth lines and most of the larger specimens also show wavy longitudinal ridges. The fossil tubes are similar to those of some modern vent vestimentiferan genera and therefore may also have a vestimentiferan origin. In addition to the coiled worm tubes, the Kambia deposit contains other ridged tubes of probable serpulid origin. The Memi, Kambia, and Kinousa deposits contain two species of small cerithioid gastropods (Fig. 4.2.5.1f), and a single epitoniid gastropod has also been found in the Memi deposit.

The Early Jurassic Figueroa VMS deposit from California is hosted by rocks of the Franciscan Complex. This is a tectonic *mélange* of ophiolitic and deep-water sedimentary rocks, and represents a fragmented accretionary prism. The Figueroa deposit contains a low-diversity fossil assemblage consisting, in order of decreasing abundance, of small, flanged worm tubes, a species of rhynchonellid brachiopod (Fig. 4.2.5.1a), and a species of ?nododelphinulid gastropod (Fig. 4.2.5.1e). The worm tubes display an external ornament of concentric growth lines and wavy longitudinal ridges (Fig. 4.2.5.1k) and are probably fossil vestimentiferan tubes, based on similarities of size and external ornamentation to the tubes of several modern vent genera.

The Middle Devonian Sibay VMS deposit from the southern Urals consists of four stacked massive sulphide lenses. The basal three of these contain intergrown vestimentiferan tubes with flanges and smaller, smooth tubes of possible polychaete affinity. In the third sulphide lens articulated specimens of a species of modiomorphid bivalve (Fig. 4.2.5.1d) co-occur with the tube worms. The Lower Devonian Oktyarbrsk deposit, also from the southern Urals, yields small pyrite tubes together with poorly preserved moulds of indeterminate brachiopods or bivalves.

The Silurian Yaman Kasy deposit from the southern Urals formed in a marginal back-arc basin and contains the oldest and most diverse fossil vent assemblage (Little *et al.* 1997). The assemblage is dominated by vestimentiferan tubes (Fig. 4.2.5.1i) and small annulated worm tubes with possible polychaete affinities (Fig. 4.2.5.1j). The shelly component of the assemblage consists of a species each of large lingulate brachiopod (Fig. 4.2.5.1b), monoplacophoran mollusc (Fig. 4.2.5.1c), indeterminate vetigastropod, and ambonychiid bivalve.

Ancient hydrothermal vent communities from other tectonic settings

Fossil assemblages have been found in a number of Palaeozoic sediment-hosted sulphide and barite deposits. These are interpreted as representing low temperature hydrothermal vent sites within sedimentary systems; some are possible ancient analogues of modern sedimented vent sites, like those in the Gulf of Mexico. Carboniferous examples include carbonate mounds with sulphide mineralization from Newfoundland, containing low-diversity, high-abundance faunas of brachiopods, trepostome bryozoans, large ?vestimentiferan tubes, conularids, crustaceans, serpulid and spirorbid polychaetes (Von Bitter *et al.* 1992); and two sedimentary ore deposits from Ireland (Tynagh and Silvermines), which contain small annulated worm tube fossils of uncertain affinity. Devonian examples include stratiform barite deposits from Nevada and Mexico, containing a genus of large rhynchonellid brachiopods and small worm tube fossils of uncertain affinity; and the Red Dog sedimentary ore deposit from Alaska which contains chert worm tubes, also of uncertain affinity.

Ancient cold seep communities

Fossiliferous ancient cold seep sites are found in similar tectonic settings to modern cold seeps, and they occur typically within deep-water siliciclastic or hemipelagic sedimentary sequences as discrete carbonate lenses with very negative $\delta^{13}C$ values and complex internal structures. These ancient cold seep fossil assemblages, like their modern equivalents, are more numerous and generally more species-rich than ancient hydrothermal vent communities (Campbell and Bottjer 1995).

The Tertiary record of cold seep faunas is extensive, with numerous sites in Japan (Pliocene and Miocene), the west coast of the USA (Mio-Pliocene, Oligocene, Eocene), Barbados, Trinidad and Venezuela (Miocene), and the Italian Apennine Mountains (Miocene 'calcari a *Lucina*'). The fossil assemblages are dominated by large articulated specimens of lucinid, thyasirid, modiolid, and vesicomyid bivalves. The more diverse sites also contain combinations of solemyid and protobranch bivalves, chitons, a variety of gastropods including trochids, neritids, provannids, naticids, buccinids, and fissurellids, serpulid worm tubes, possible vestimentiferan tubes, and siliceous sponges.

Cretaceous and Jurassic cold seep faunas are less well known but have been found in the western interior of the USA (Campanian 'tepee buttes'), California (Tithonian,

Fig. 4.2.5.1 Selected fossils from ancient hydrothermal vent communities. (a) Rhynchonellid brachiopod *Anarhynchia* cf. *gabbi*, pedicle valve exterior; Early Jurassic, Figueroa deposit, California, ×2. (b) Lingulate brachiopod *Pyrodiscus lorrainae*, pedicle valve exterior; Silurian, Yaman Kasy deposit, Russia, ×1.5. (c) Monoplacophoran *Thermoconus shadlunae*, lateral view; Yaman Kasy deposit, ×1. (d) Modiomorphid bivalve *Sibaya ivonovi*, slightly oblique view of articulated specimen, anterior to left; Middle Devonian, Sibay deposit, Russia, ×1.5. (e) ?Nododelphinulid gastropod, oblique apical view; Figueroa deposit, ×3. (f) Cerithioid gastropod, lateral view; Cretaceous, Memi deposit, Cyprus, ×10. (g) ?Vestimentiferan tube; Memi deposit, ×10. (h) ?Vestimentiferan tube; Cretaceous, Kapedhes deposit, Cyprus, ×10. (i) Vestimentiferan *Yamankasia rifeia* tube; Yaman Kasy deposit, ×1. (j) Polychaete worm *Eoalvinellodes annulatus* tube; Yaman Kasy deposit, ×3. (k) ?Vestimentiferan tube, Figueroa deposit, ×5.

Hauterivian, and Albian), Arctic Canada (Albian), northern Japan (Cenomanian and Albian), Antarctica (Tithonian), and south-east France (Oxfordian). Many of these assemblages contain similar taxa to the Tertiary sites, including lucinids, modiolids and solemyids, various gastropods, and serpulid and possible vestimentiferan worm tubes, but vesicomyids are less common, occurring only in the Japanese sites. Another very important difference is that articulate brachiopods, some very large, are abundant in a number of the assemblages, such as a terebratulid species from the Canadian Arctic, and two rhynchonellid genera from California and Europe.

A small number of anomalous Palaeozoic sedimentary structures with fossils have been interpreted as being formed by cold seepage: mid-Devonian mud mounds from Morocco contain dense accumulations of articulated anomalodesmatid bivalves; mid-Ordovician sediment mounds from Canada contain low-diversity faunas dominated by strophomenid brachiopods and ramose bryozoans; early Ordovician ophicalcites, also from Canada, have possible microbial textures and may be the oldest known chemosynthetic communities.

Evolutionary significance

The fossil record of hydrothermal vents and cold seeps shows that communities of animals dependent on chemosynthetic bacteria have been present in the oceans at least since the early Ordovician, and that these communities lived under the same environmental conditions found at modern vent and seep sites. These ancient vent and seep communities appear to have always contained significant numbers of animals with endosymbiotic relationships. In general the Tertiary hydrothermal vent and cold seep communities are comparable to modern communities in taxonomic structure, but these similarities become less apparent in the Mesozoic and Palaeozoic where brachiopods, for example, become increasingly important constituents (Campbell and Bottjer 1995). None of the Palaeozoic vent or seep taxa are directly ancestral to modern vent and seep species, apart from possibly the vestimentiferan and polychaete worms, so it seems very unlikely that modern vent and seep communities contain Palaeozoic 'relics'. The temporal changes in hydrothermal vent and cold seep ecosystems indicate that they were more dynamic taxonomically through time than was previously thought, and that these environments were not refuges from extinction (Little *et al.* 1998).

References

Campbell, K.A. and Bottjer, D.J. (1995) Brachiopods and chemosymbiotic bivalves in Phanerozoic hydrothermal vent and cold seep environments. *Geology* **23**, 321–324.

Little, C.T.S., Herrington, R.J., Maslennikov, V.V., Morris, N.J. and Zaykov, V.V. (1997) Silurian hydrothermal-vent community from the southern Urals, Russia. *Nature* **385**, 146–148.

Little, C.T.S., Herrington, R.J., Maslennikov, V.V., Morris, N.J. and Zaykov, V.V. (1998) The fossil record of hydrothermal vent communities. In: R.A. Mills and K. Harrison, eds. *Modern ocean floor processes and the geological record*, pp. 259–270. Geological Society of London Special Publication no. 148.

Sibuet, M. and Olu, K. (1998) Biogeography, biodiversity and fluid dependence of deep-sea cold-seep communities at active and passive margins. *Deep Sea Research II* **45**, 517–567.

Tunnicliffe, V. (1992) The nature and origin of the modern hydrothermal vent fauna. *Palaios* **7**, 338–350.

Von Bitter, P.H., Scott, S.D. and Schenk, P.E. (1992) Chemosynthesis: an alternative hypothesis for Carboniferous biotas in bryozoan/microbial mounds, Newfoundland, Canada. *Palaios* **7**, 466–484.

4.2.6 Zooplankton

S. RIGBY and C.V. MILSOM

Introduction

Zooplankton have the widest geographical spread and greatest numerical abundance of any group of animals. They are important contributors to global biomass and to the chemistry of the oceans. Their fossil record is of long duration, and they must have functioned in these roles throughout time. However, analyses of fossil plankton are hampered because preservation is generally poor due to postmortem transport and because morphological adaptations, particularly the reduction of skeletal material, restrict fossilization potential.

Functional innovations appeared quickly in the plankton: there must have been effective and frequent movement of organisms into the plankton from the benthos. This movement into the plankton seems to have been independent of any biological or environmental forcing mechanism (Rigby and Milsom 1996). There is no temporal pattern to plankton recruitment. Although the cohort of plankton was increased by migration in a random and sporadic fashion, subsequent radiations and extinctions within this cohort closely reflected events in the benthos (Signor and Vermeij 1994). Mass extinctions affected organisms across ecological groups and province boundaries, and at a species level the plankton seems to have been particularly sensitive to changes in the oceanic environment.

Evolutionary patterns

Most zooplankton have been recruited into their environment and mode of life from benthic ancestors. This recruitment can be demonstrated directly for some groups, such as graptolites, ostracods, and foraminiferans. It can be inferred for others on the basis of their phylogeny, the best example being the cnidarians, which are primitively benthic. Migration into the plankton could take place through the movement of adults, as in gastropods and ostracods, or by neoteny, as was the case for graptoloids. The wide distribution of planktic larval stages throughout the invertebrates is a preadaptation to becoming planktic.

Recruitment to the plankton occurred throughout geological time and seems to have been possible in any period; it is neither confined to, nor favoured by, environmental change or biological crises (Fig. 4.2.6.1). Migration into the plankton may have been facilitated by the apparent lack of competitive exclusion in planktic systems. This is exemplified by the paradox of the plankton—that similar species can coexist indefinitely. Suggestions that evolution of the plankton has been controlled largely by abiotic factors contrast with the argument that predation is a vital 'top-down' cause of selection in the benthic system and give much scope for future research and debate.

Precambrian and Palaeozoic

It is generally agreed that medusoid cnidarians constituted the first metazoan plankton. Although it has been assumed that these were part of the Ediacaran faunas, there are also possible occurrences in older rocks. However, the Precambrian history of zooplankton is poorly understood. The appearance of metazoan hard parts and their subsequent Cambrian radiation were closely mirrored by diversifications and rapid rates of evolution in the plankton. The assemblage of zooplankton in the Burgess Shale begins to approach the diversity of modern plankton communities and probably contains five of the eight major phyla of modern macrozooplank-

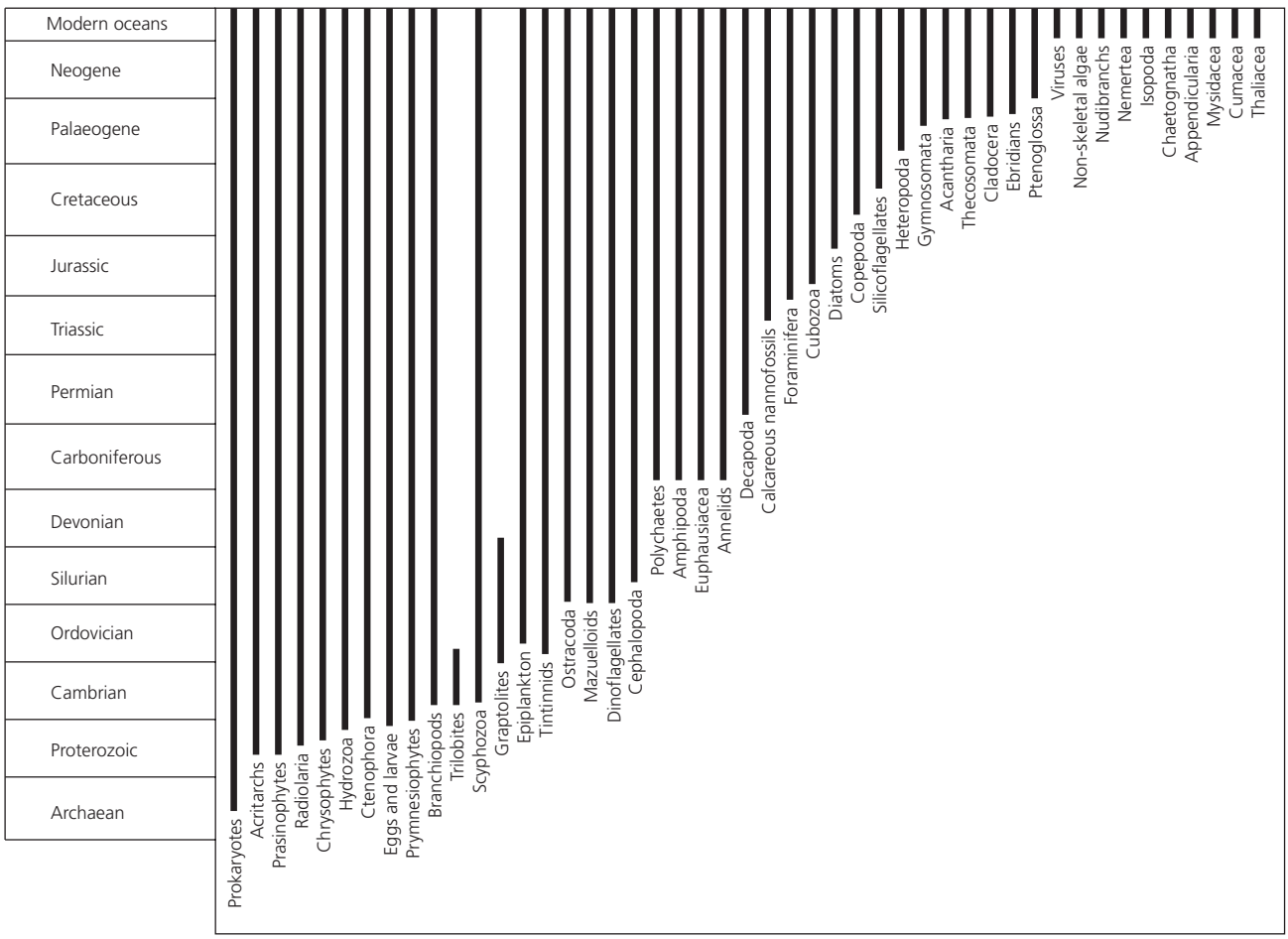

Fig. 4.2.6.1 Origination of zooplankton and the major groups of phytoplankton.

ton (although the taxonomic affinities of these fossils are often disputed). This high diversity indicates that, at least by Middle Cambrian times, the Cambrian radiation had reached the pelagic realm. Increasing diversity is also reflected in the occurrence of planktic organisms in pelagic black shales of Cambrian age. Middle Cambrian rocks of Canada yield the filtering apparatus of a branchiopod-like crustacean which is likely to have been planktic for at least part of its life cycle. These crustaceans would have been up to 10 mm long and the regularity of their filtering nets suggests a planktic source of food. Possible Cambrian radiolarians have been identified but they are rare and microzooplankton appear to have been largely absent from Cambrian seas. Larval forms must have been present, though perhaps in less abundance than today. The most reliably inferred of these are the larvae of pterobranchs and their sister group, graptolites, both of which had evolved by the Middle Cambrian.

Zooplankton continued to migrate into the pelagic realm through the Late Cambrian and Early Ordovician. Radiolarians became dominant components of the Ordovician microzooplankton. With their diversification, silica began to be partitioned between shallow and deep water for the first time. Their distribution and changes in their rate of evolution correlate well with similar changes shown by graptoloids. Tintinnids appeared in the Ordovician but were rare. Ordovician chitinozoans may represent the first larval stages preserved within the plankton. The most significant of these new zooplankton are probably the graptoloids, which evolved by neoteny from benthic graptolites at the base of the Ordovician period. These colonial hemichordates radiated quickly into a wide variety of shapes, and presumably of niches. Trilobites with a likely pelagic habit include *Opipeuter, Carolinites, Girvanopyge, Selenopeltis,* the Bohemillidae, and the cyclopygids (Fortey 1985). The full complement of Lower Palaeozoic plankton may have included at least one species of inarticulate brachiopod. Ostracods migrated into the planktic habitat during the Silurian. Cnidarians constituted a significant fraction of the zooplankton of the Lower Palaeozoic. The ctenophores *Palaeoctenophora* and *Archaeocydippida* are recorded from the Devonian Hunsrück Slate.

The rise in planktic diversity amongst metazoans parallels the rise of the Palaeozoic fauna (Signor and Vermeij 1994). The cause of this increase in planktic diversity may have been the use of the pelagic realm as a refuge from bioturbation and predation on the sea floor. Although the Lower Palaeozoic was generally a time of high plankton diversity, there is evidence for a major extinction of plankton synchronous with the mass extinction of benthos at the end of the Ordovician (see Section 2.4.2).

In contrast to previous periods, the Upper Palaeozoic was a time of low plankton diversity and muted primary productivity. Late Devonian extinctions particularly affected the plankton and the system was unable to recover until the Jurassic. Until the final 2 million years of the Devonian, diversity was maintained by high rates of origination. When this rapid evolution ceased, diversity fell quickly. The ecosystem collapsed suddenly and the effect was widespread or even global.

The long period of impeded plankton development in the late Palaeozoic is a puzzle. It is possible that the spread of vascular plants caused carbon, nitrogen, and phosphorus to be progressively retained on land. As marine nutrients were gradually lost into deep-sea sediments, a major crisis was precipitated. An alternative view is that the development of land ecosystems during this period led to greater nutrient run-off and increased primary productivity. Prolonged disequilibrium in terrestrial systems may have contributed to the paucity of plankton, or a diverse form of primary plankton producer may have been present but not preserved, although both of these suggestions seem improbable.

In the Early Devonian a noticeable change in faunal composition occurred which coincides approximately with the point at which planktic graptoloids became extinct and the ammonoids appeared. These changes in the planktic cohort, at a relatively high trophic level, may have contributed to changes in the system as a whole. Radiolarian diversity fell dramatically towards the end of the Carboniferous and recovered gradually through the Permian and Early Triassic.

However, some elements of the plankton suffered no noticeable effect. Chondrophorines occur throughout the Upper Palaeozoic, sometimes in great abundance. Over 6000 specimens of soft-bodied cnidarians have been reported from the Essex fauna (the marine assemblage of the Mazon Creek biota) and these include representatives of all the modern planktic scyphozoan orders. It is also likely that new recruits appeared in the zooplankton even through this time of low productivity. The Granton Sandstone contains the first planktic polychaete worm *Eotomopteris aldridgei*. Carboniferous aeschronectid crustaceans may have been pelagic. The eumalacostracan crustacean *Waterstonella*, the most common Granton crustacean, does not have walking limbs, is poorly mineralized, occurs in swarms, and was small and probably pelagic. Long-lived planktic larvae are predominantly found in clades with a late Palaeozoic or more recent origin (Signor and Vermeij 1994), making it likely that their importance in the plankton increased steadily through this time interval.

Mesozoic

The Mesozoic saw a massive radiation of microplankton,

and probably also of macroplankton. Innovation of skeletal type, particularly the radiation of calcareous microplankton, had far-reaching implications throughout the water column. It is postulated that continental break-up, with the consequent partitioning of oceans, encouraged diversification at this time (Lipps 1993). Mesozoic zooplankton included diverse species of radiolarians, especially nassellarians. Tintinnids are rare elements of the plankton of most geological systems, but they radiated significantly across the Jurassic–Cretaceous boundary, becoming rare once more in the Late Cretaceous. The peak of microfossil diversity (excluding dinoflagellates) for the Phanerozoic was reached in the Cretaceous. Planktic foraminiferans appear in rocks of Middle Jurassic age. Genetic analysis suggests that a planktic habit has evolved more than once in the group, and it may be that this transition is a simple one for such small, chambered forms.

The Mesozoic record of macrozooplankton is sparse, although chondrophores persisted. Crustaceans were present in the Mesozoic plankton but evidence for their occurrence is limited to Lagerstätten. A planktic lifestyle is proposed for the bivalve *Bositra radiata*. Decapod crustaceans, gastropods, and most larvae have post-Palaeozoic origins in the macrozooplankton (Signor and Vermeij 1994), but identifying the timing of their arrival is problematic. It is likely that all Mesozoic recruits were migrants from the benthos (Rigby and Milsom 1996).

Most elements of the plankton show high levels of extinction across the Cretaceous–Tertiary boundary. A rapid fall in primary productivity resulted in mass starvation higher up the food chain. Survivors amongst the zooplankton were preferentially small species and survivors tended to be below average size for their species (Paul and Mitchell 1994). Extinction affected all planktic groups but was most severe for open-water surface dwellers and less so for inhabitants of the deep oceans. Both foraminiferans and calcareous nannoplankton were devastated by the end-Cretaceous event, but their patterns of extinction and subsequent recovery are different. Nannoplankton suffered later extinction and later recovery than did foraminiferans, leading to the suggestion that the zooplankton were killed by a collapse in the availability of food, whereas the phytoplankton survived in very low numbers and were subsequently outcompeted by new Cenozoic forms.

Cenozoic

During the Cenozoic, plankton diversity in most groups recovered partially from the end-Cretaceous, but did not return to its former levels. Most microplankton display high diversity in the Paleocene–Eocene and Miocene, with low diversity in between. Those planktic taxa which survived extinctions generally displayed simple morphologies, and subsequent radiations produced iterative evolution, with complicated forms arising from these simple stocks.

Amongst zooplankton the dominant forms of the Cenozoic were foraminiferans, radiolarians, and tintinnids. Radiolarians show a conspicuous faunal change between the Mesozoic and Cenozoic and their frustules tended to become lighter due to the increased competition for silica engendered by the radiation of diatoms. Heteropod and thecosome gastropods became planktic by migration from benthic habits prior to the Eocene, and most other planktic gastropods, including sea slugs, are also probably Cenozoic in origin. All of these groups evolved from benthic ancestors, most likely by adult migration. Most of the extant groups of planktic crustaceans lack a fossil record but probably migrated into the plankton in the Cenozoic. Salps and thaliaceans are a major soft-bodied component of modern planktic ecosystems but they have no fossil record and their time of origin is unknown. It is likely that they formed part of the Cenozoic plankton, and possibly the plankton of earlier eras.

References

Fortey, R.A. (1985) Pelagic trilobites as an example of deducing the life habits of extinct arthropods. *Transactions of the Royal Society of Edinburgh* **76**, 219–230.

Lipps, J.H. (1993) *Fossil prokaryotes and protists*. Blackwell Scientific Publications, Oxford.

Paul, C.R.C. and Mitchell, S.F. (1994) Is famine a common factor in mass extinctions? *Geology* **22**, 679–682.

Rigby, S. and Milsom, C.V. (1996) Benthic origins of zooplankton: an environmentally mediated macroevolutionary effect. *Geology* **24**, 52–54.

Signor, P.W. and Vermeij, G.J. (1994) The plankton and the benthos: origins and early evolution of an evolving relationship. *Paleobiology* **20**, 297–320.

4.2.7 Terrestrial Palaeobiogeography

R.S. HILL

Introduction

Biogeography is a science steeped in the past, so the reasons for distribution patterns among the living biota are rarely directly observed. The terrestrial biota is extraordinarily complex, and few organisms share exactly the same distribution. While the processes that govern these distributions are relatively simple, they

have acted in many different ways, over different time scales, and with different controls, leading to the observed complexity.

Biogeographical processes

If an organism is spatially distributed in a way that warrants explanation, there must have been dispersal events, where organisms presumably migrated across pre-existing barriers, and/or vicariance events, where the formation of barriers fragmented the ranges of once continuously distributed species. These alternatives represent past events that cannot be directly observed. For each case examined, data must be gathered to test hypotheses formulated to explain current distributions. These data can take several forms. A major recent advance has been the increasing accuracy of phylogenetic reconstructions of complex living taxa using cladistic methodology. If the evolutionary branching points can be predicted, the biogeographical history of a monophyletic group of species can be reconstructed by comparing the relative positions of these branching points with known disjunctions in their distribution. However, there are several reasons why species-rich taxa with complex distributions rarely yield simple explanations from this approach. Chief amongst these are that the reconstructed phylogeny may be inaccurate because of poorly understood data, and the current distributions may be due to a combination of vicariance and dispersal events that do not yield easily understood histories.

The fossil record is an important additional resource, providing at least two unique forms of data. Firstly, fossils provide unequivocal data on past distributions, which must be consistent with any explanation of the distribution of related living taxa. Secondly, fossils may provide an important test of proposed phylogenetic relationships, although this can be difficult, since fossils may represent extinct phylogenetic lines as well as direct ancestors of living taxa.

Controls on biogeographical processes

No matter what process is involved in dispersing organisms, there are physical controls on their distribution. The most obvious of these is climate. For example, if a plant has seeds that are wind dispersed over great distances, there is a good chance that many will land in climatically unsuitable places for that species and they will not survive there. Vicariance events can also be subjected to this kind of distributional control, sometimes over much longer periods of time. Australia and Antarctica provide an excellent example. Since they separated ≈40 Ma, Australia has drifted northwards through more than 20° of latitude, has dried out enormously, and has undergone major temperature changes, while Antarctica has been plunged into severe glacial climates that few large organisms have survived. Many species that were originally present on both continents were separated by the vicariance event. Most are now absent from one or both continents because of later climate change. Another important control on dispersal is the need for establishment space. The most dramatic examples of successful modern dispersal occurred on land that was not fully occupied at the time of colonization because of major physical disruption, thus providing space for new colonizers to establish (e.g. Krakatau).

Nothofagus as an example of biogeographical patterns

Biogeographical patterns are best explained by example. The distribution of the Southern Hemisphere terrestrial biota during and following the fragmentation of Gondwana is an interesting and complex case. There are no general examples, since every taxon has a unique history. However, some organisms probably give a better than average guide to the patterns and processes involved, and the angiosperm genus *Nothofagus* (southern beech) is one of these.

Nothofagus is prominent in the biogeographical literature because of its usually impressive size, its dominance in many forests, its classic southern distribution, and the supposed lack of long-distance fruit dispersal, which meant dispersal was assumed to be land-based. Additionally, its fossil record is unrivalled in the Southern Hemisphere in complexity and completeness, and therefore it might be expected that reconstruction of its history should be straightforward. This is not the case, for reasons outlined below.

Nothofagus is now mainly distributed around the Pacific, with 26 of the 35 species occurring in New Guinea, New Caledonia, New Zealand, and Australia. However, this has not always been the case, and in order to explain the current distribution and diversity of *Nothofagus*, its phylogenetic history must be examined, along with the detail of its fossil record.

Classification

Nothofagus was originally assigned to the Fagaceae, with an assumed close relationship to *Fagus*. This created major biogeographical problems, since *Fagus* is strictly northern hemispheric, whereas *Nothofagus* is southern. Recently *Nothofagus* has been moved to the monogeneric family Nothofagaceae, and its nearest living relatives may be in the Betulaceae rather than Fagaceae, but this does not assist with biogeographical reconstruction, since Betulaceae is also confined to the Northern Hemisphere.

The infrageneric classification of *Nothofagus* (Hill and Read 1991) is critical to biogeographical reconstruction, and was resolved using pollen morphology,

general morphology, and cladistic analysis of morphological and molecular characters. The subgeneric limits are well defined, but the relationships among them and among species within them are not well understood. This is partly because the majority of *Nothofagus* diversity occurred in the past, and research based mainly on extant species is likely to give an imperfect result.

Possible centres of origin

Many places of origin and migration routes have been invoked for *Nothofagus*, but most have been rejected (Hill and Dettmann 1996). Pollen data support the southern South America–Antarctic Peninsula region as a centre of origin for *Nothofagus* in the Early Campanian (Dettmann *et al.* 1990). This was part of the 'Weddellian Province', which extended from southern South America along the Antarctic coastline to south-eastern Australia and New Zealand, as a continual coastal environment bordered by shallow seas. At high southern latitudes, Cretaceous–Palaeogene *Nothofagus* is associated with, or preceded by, macrofossils that are regarded as fagaceous or betulaceous (e.g. McLoughlin *et al.* 1995). This places these now strictly northern families in the Southern Hemisphere at the right time, but does not tell us how they got there. The link may have been via South America (the 'marsupial route'), or possibly the ancestral complex for Nothofagaceae, Fagaceae, and Betulaceae occurred in South-East Asia. Attention has recently focused on probable Late Cretaceous-Palaeogene biotic interchange between South-East Asia and Australia, where a complex of continental fragments may have provided a 'stepping stone' path since the Early Cretaceous, and especially in the Late Cretaceous and Palaeogene (Hill and Dettmann 1996) (Fig. 4.2.7.1).

Nothofagus is not among the several potential exploiters of this route recovered from the fossil pollen record, but if its immediate ancestor existed in the South-East Asian–Australian region it probably produced generalized pollen distinct from *Nothofagus* (Hill and Dettmann 1996) and its presence may not have been detected. If this ancestral complex existed it may have given rise to the Betulaceae and Fagaceae north of the equator in South-East Asia, where the Betulaceae has its earliest fossil record. Part of this complex may have migrated to the Weddellian Province, there to evolve into *Nothofagus*. The presence of angiosperm leaves of probable fagaceous or betulaceous affinity in the Cenomanian of north-eastern Australia (McLoughlin *et al.* 1995), well before the first fossil record of *Nothofagus*, may indicate the presence of this ancestral complex near its Asian source before it reached the Weddellian Province. 'Ancestral' *Nothofagus* pollen has been recorded in latest Santonian and Campanian sediments offshore from northern Australia (Hill *et al.* 1996). While the Santonian occurrences may represent contamination from younger strata, the alternative of an early occurrence of '*Nothofagus*' pollen in the Australia–South-East Asia region, perhaps produced by the same parent plants as the leaves described by McLoughlin *et al.* (1995), cannot be discounted.

Reconstruction of the early history of *Nothofagus* relies heavily on palynology. Fossil *Nothofagus* pollen is often so common that its absence is important evidence, and has been used to conclude that it was never present in Africa or India (Hill and Dettmann 1996). Eight pollen types have been identified among fossil *Nothofagus*, only four of which are extant (Dettmann *et al.* 1990). Two of the extinct types are considered ancestral by Dettmann *et al.* (1990). Ancestral type (a) pollen first appears in Early Campanian sediments and then occurs over wide areas of southern Gondwana. Ancestral type (b) pollen first appears in Middle Campanian sediments at very high southern latitudes.

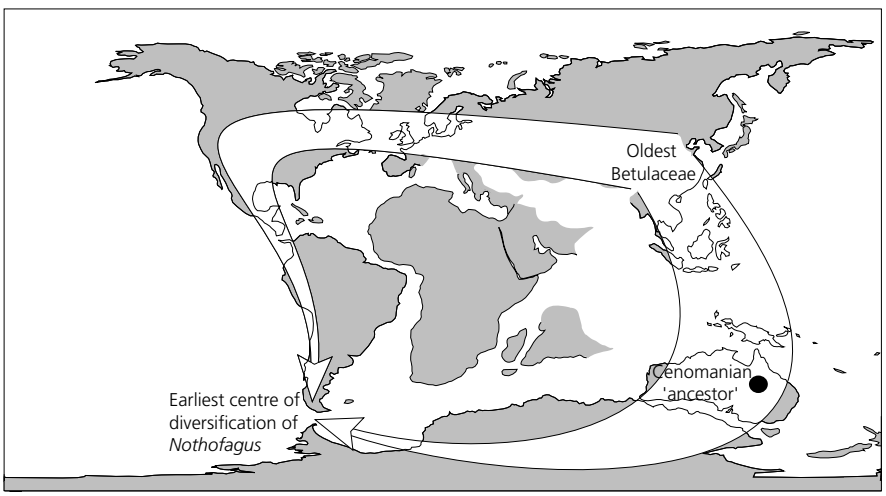

Fig. 4.2.7.1 The world ≈ 100 Ma showing the position of the oldest Betulaceae fossils (China) and possible routes for elements of this complex to reach the place where *Nothofagus* first diversified (southern South America–Antarctic Peninsula region).

Diversification and migration

Soon after these 'ancestral' *Nothofagus* pollen types appeared, rapid diversification events that were spatially and temporally distinct occurred at times of high volcanic and tectonic activity. This suggests an ecological response similar to many extant species that occur in areas of high natural disturbance (Dettmann *et al.* 1990). Pollen of all extant subgenera first appear in the Late Campanian of the Antarctic Peninsula and the Maastrichtian of southern South America. This region was a centre of Late Cretaceous diversity of *Nothofagus* and several other taxa. The significantly younger appearance of the extant subgenera in southern Australia and New Zealand suggests a migrational lag and pathways through western Antarctica (Dettmann *et al.* 1990) (Fig. 4.2.7.2).

'Ancestral' *Nothofagus* pollen was the only type present in New Zealand when it separated from Antarctica, but later the extant subgenera appeared. There is compelling palynological and molecular evidence that *Nothofagus* repeatedly colonized New Zealand by long-distance dispersal during the Cenozoic (Fig. 4.2.7.3). It is possible that New Zealand was completely inundated by the sea during the Late Oligocene, which would mean that all *Nothofagus* currently on New Zealand (along with the rest of the biota) is the result of long-distance dispersal (Pole 1994). Long-distance dispersal of *Nothofagus* may have been important in other areas, but data are lacking to test this at present.

The subgenus *Brassospora* first appeared in the Antarctic Peninsula–southern South America region, although it is absent there post-Oligocene (Dettmann *et al.* 1990). It diversified during the Eocene–Oligocene in the Australia–New Zealand region. This diversification included a massive increase in the amount of pollen as well as in species numbers, but it is not clear whether this represents a major increase in *Nothofagus* biomass or an evolutionary event leading to more prolific pollen-producing species (Hill and Dettmann 1996). If the latter is true, then the usual interpretation of a major vegetation shift at this time may be incorrect. Most *Brassospora* species became extinct in southern Australia and New Zealand during the late Cenozoic, presumably in response to climatic change. The arrival of subgenus *Brassospora* in its current range of New Guinea and New Caledonia occurred late in the history of *Nothofagus*, presumably as a result of range change and restriction in response to massive climate change in Australasia (Fig. 4.2.7.3). The New Caledonian occurrence may be the result of long-distance dispersal, probably from New Zealand.

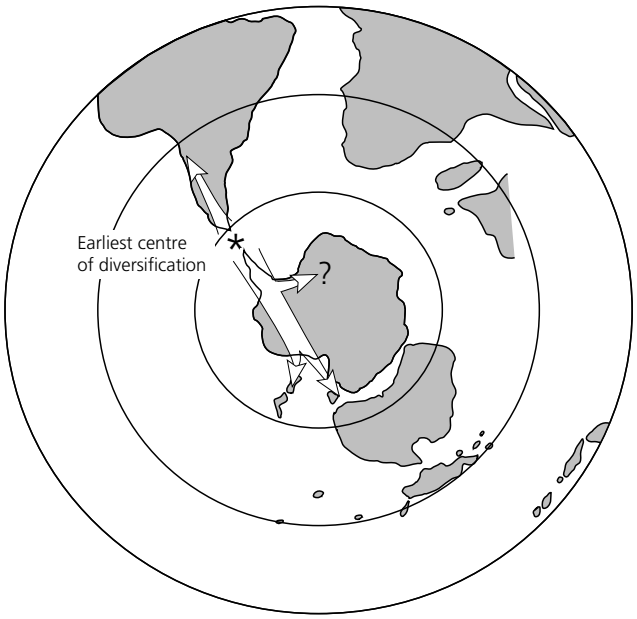

Fig. 4.2.7.2 The Southern Hemisphere in the Late Cretaceous showing the initial routes of *Nothofagus* out from its centre of diversification.

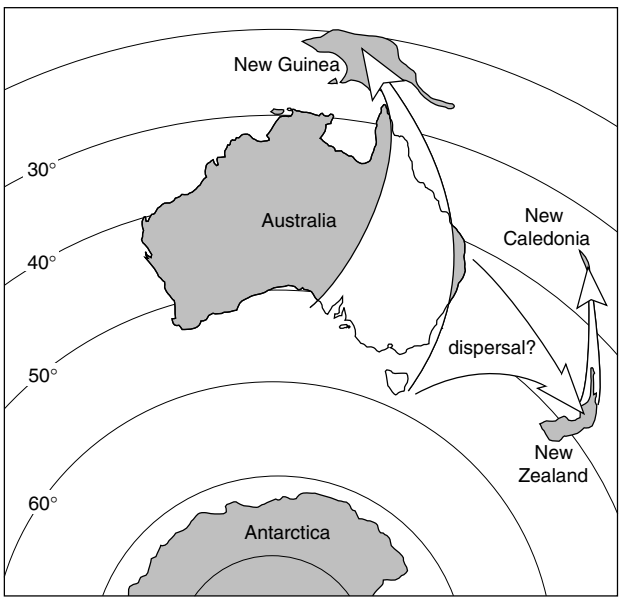

Fig. 4.2.7.3 Australasia during the Early Miocene (≈20 Ma), showing the route by which subgenus *Brassospora* moved northwards through Australia to New Guinea and probably from New Zealand to New Caledonia as climate changed. The probable long-distance dispersal route of several species of *Nothofagus* (from all extant subgenera) from Australia to New Zealand is also shown.

Conclusion

Nothofagus has a complex history, combining obvious

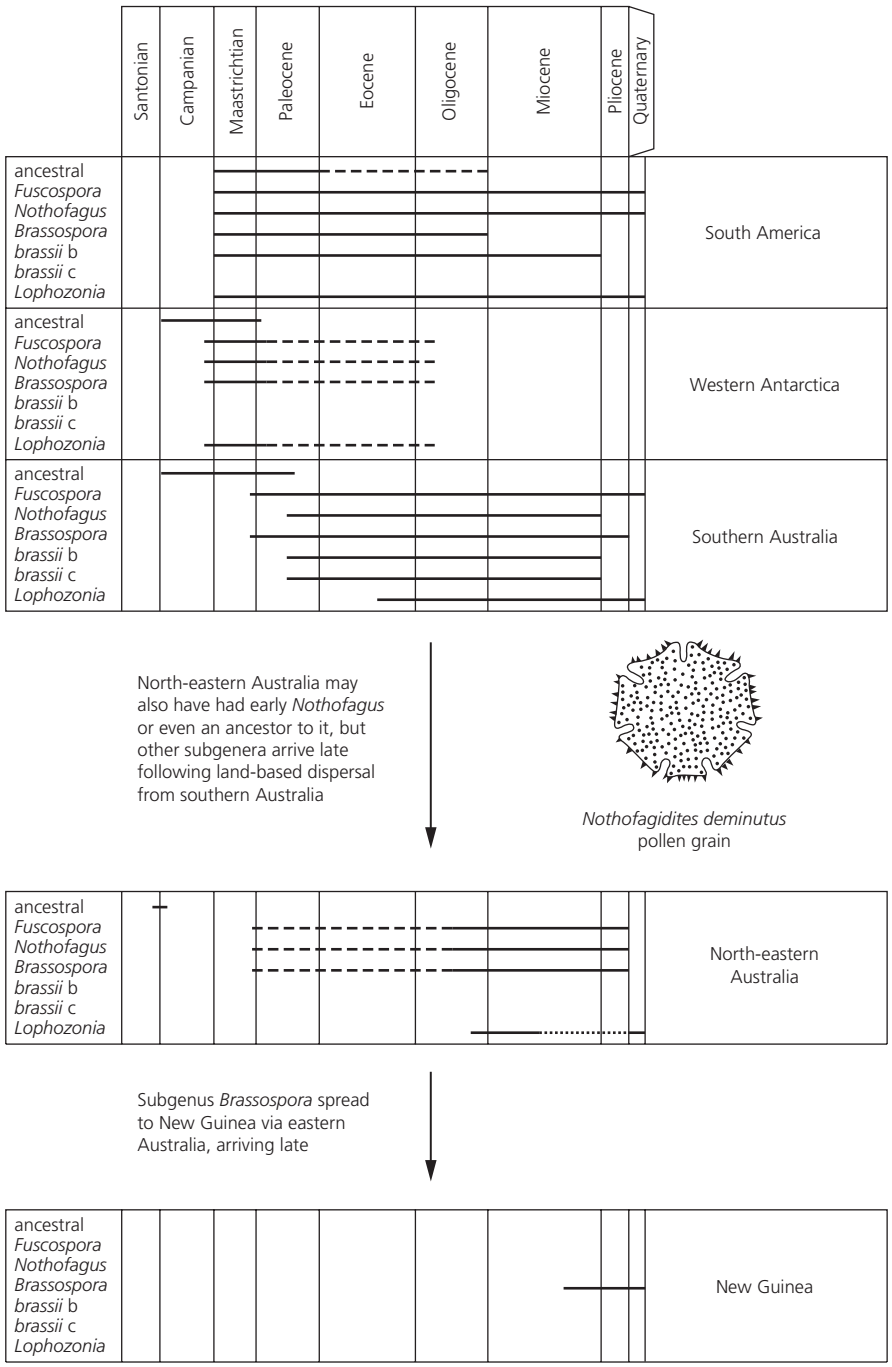

Fig. 4.2.7.4 Pollen ranges of the 'ancestral' type and the other six pollen groups identified by Dettmann *et al*. (1990). South America, western Antarctica, and southern Australia represent a possible centre of origin of *Nothofagus*, with vicariance events separating the populations that had spread across high southern latitudes by land-based dispersal. Modern subgeneric names have been used where applicable. The pollen ranges shown here form the basis of most of the palaeobiogeography discussed in the text. The illustrated fossils are pollen of *Nothofagidites deminutus* (*brassii* c), a leaf of *Nothofagus maideni* (subgenus *Lophozonia*), and a cupule of *Nothofagus bulbosa* (subgenus *Nothofagus*). (Pollen range data adapted from Dettmann *et al*. 1990.) (*Continued)*

vicariance events during the rifting of Gondwana with probable long-distance dispersal, at least from Australia to New Zealand, and maybe from Australia and/or New Zealand to New Caledonia (Fig. 4.2.7.4). Other long-distance dispersal events may also have occurred. Its distribution has been heavily influenced by changing Cenozoic climates and probably by other events such as changing disturbance regimes and changing photoperiods as continents shifted latitudinally. Its early history and its immediate ancestor are still uncertain, but must involve a long migration from the Northern Hemisphere. While *Nothofagus* stands as a particularly interesting example of palaeobiogeography, the important message is that its history is unique, and attempts to generalize from it, or any other taxon, are likely to fail. For example, recent research on Proteaceae pollen has shown that this family, which is about the same age as *Nothofagus* and shares much of its southern distribution, has a markedly different early history (Askin and Baldoni 1998).

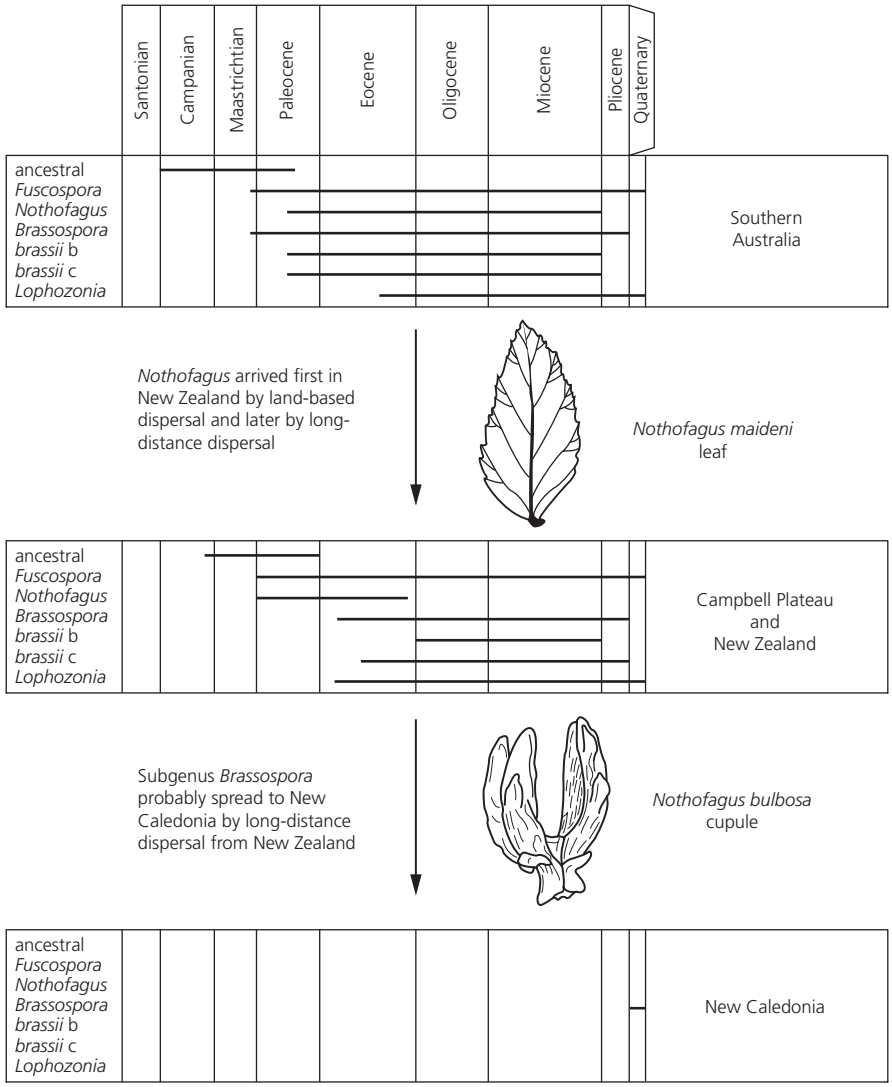

Fig. 4.2.7.4 (*Continued*)

References

Askin, R.A. and Baldoni, A.M. (1998) The Santonian through Paleogene record of Proteaceae in the southern South America–Antarctic Peninsula region. *Australian Systematic Botany* **11**, 373–390.

Dettmann, M.E., Pocknall, D.T., Romero, E.J. and Zamaloa, M.D.C. (1990) *Nothofagidites* Erdtman ex Potonié, 1960: a catalogue of species with notes on the paleogeographic distribution of *Nothofagus* Bl. (southern beech). *New Zealand Geological Survey Paleontological Bulletin* **60**, 1–79.

Hill, R.S. and Dettmann, M.E. (1996) Origin and diversification of the genus *Nothofagus*. In: T.T. Veblen, R.S. Hill and J. Read, eds. Nothofagus *ecology and evolution*, pp. 11–24. Yale University Press, New Haven, Connecticut.

Hill, R.S. and Read, J. (1991) A revised infrageneric classification of *Nothofagus* (Fagaceae). *Botanical Journal of the Linnaean Society* **105**, 37–72.

Hill, R.S., Jordan, G.J. and Macphail, M.K. (1996) Paleoecology of *Nothofagus* in Australia. In: T.T. Veblen, R.S. Hill and J. Read, eds. Nothofagus *ecology and evolution*, pp. 182–199. Yale University Press, New Haven, Connecticut.

McLoughlin, S., Drinnan, A.N. and Rozefelds, A.C. (1995) A Cenomanian flora from the Winton Formation, Eromanga Basin, Queensland, Australia. *Memoirs of the Queensland Museum* **38**, 273–313.

Pole, M.S. (1994) The New Zealand flora—entirely long-distance dispersal? *Journal of Biogeography* **21**, 625–635.

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4.2.8 Epibionts

H.L. LESCINSKY

Introduction

Epibionts are organisms that lived on other organisms. They are easily overlooked, but epibionts form a significant part of the species pool in many marine environments. In addition, multispecies epibiont assemblages are often exceptionally good representations of 'biological communities'. They preserve ecological information that is usually lost in fossil assemblages, including competitive interactions, abundance, diversity, recruitment strategies, ecological succession, and niche partitioning. Long-term patterns of community change and ecological trends can also be examined in epibiont communities by comparing examples from similar facies and hosts over successive geological periods.

Some epibiont hosts, such as brachiopods, are relatively ephemeral, and multispecies epibiont assemblages found on undegraded, articulated valves probably represent epibionts that settled, lived, and interacted in ecological time. These assemblages are close approximations of the original biological communities. Abraded shells, skeletons of robust taxa such as stromatoporoids and oysters, and hardgrounds are more likely to preserve complex records of multiple generations of epibiont colonization. Even on these robust substrates, the relative timing of colonization by different organisms can be interpreted from overgrowth and cross-cutting relationships. Thus, time-averaging (see Section 3.2.7) is much less of a problem in interpreting fossil epibiont suites than it is for typical soft-bottom assemblages.

Space and biomass in most epibiont communities are dominated overwhelmingly by sessile suspension feeders, including encrusters which cement on host shell surfaces, and endobionts (borers) which excavate living spaces within mineralized shells. Most epibionts are generalists and colonize their host shells primarily as patches of hard substrate, often on muddy bottoms where inorganic hard substrates are rare. Epibiont taxa that settle quickly on ephemeral substrates, such as shells, generally have preservable skeletons; soft-bodied encrusters, such as sponges and tunicates, become increasingly common as substrates are exposed for longer periods of time. Epibiont communities also contain fleshy and coralline algae and several less well-preserved invertebrate guilds, including grazers, nestlers (scavengers/suspension feeders), and mobile predators. The structure and composition of these guilds is much more difficult to reconstruct than suspension-feeding guilds and must be inferred from information such as grazing traces, predation marks on epibiont skeletons, and associated fossils.

Ecological information

Abundance is particularly difficult to investigate in most fossil assemblages, but in epibiont and other encruster assemblages both relative and absolute abundance can be measured. Individual epibionts can be counted in a standard unit of area, or compared with other species for a measure of relative abundance. The percentage of surface area covered by various epibionts indicates resource utilization and is useful in comparing the abundance of solitary and colonial epibionts. Abundance data allow the calculation of an ecological diversity measure such as the Shannon Index, which can supplement species-richness counts.

Space is often a limiting factor for sessile suspension feeders, and examples of one epibiont overgrowing another provide evidence of competitive interactions and hierarchies. Overgrowth ability correlates largely with colony form, and abundance and competitive ability are not always related. On Silurian crinoid calices, for example, the most abundant encrusting bryozoan is the most likely to have been overgrown (Liddell and Brett 1982). Ecological succession arises from either competitive overgrowth or growth following the death of short lived epibionts. In Palaeozoic epibiont communities, for example, colonial bryozoans did not overgrow the apertures of live spirorbid worms and cornulitids, but often encrusted over them once they were dead (Lescinsky 1997).

Sessile epibiont taxa are locked in place on shells and therefore their locations may be used to infer recruitment patterns. Gregarious recruitment may result in individuals clumped on the available substrate, or selectively distributed on host shells from a particular stratigraphic horizon. Niche partitioning can also be investigated by examining the positions of epibionts on shells. Larvae of many Recent invertebrates actively select a settlement site and this selectivity contributes to the final epibiont assemblage. Encrusting bryozoan species on disarticulated bivalve shells differ between rough and smooth surfaces, shell ridges and grooves, and convex and concave surfaces (Ward and Thorpe 1989). Similar selectivity occurred on Devonian shells where some epibionts, such as various *Hederella* species, favoured cryptic surfaces, whereas auloporid corals, craniid brachiopods, and sheet bryozoans favoured exposed surfaces (Kesling *et al.* 1980).

Geological history

During the Cambrian, epibionts, like other suspension feeders, were rare (Fig. 4.2.8.1). This rarity may reflect a

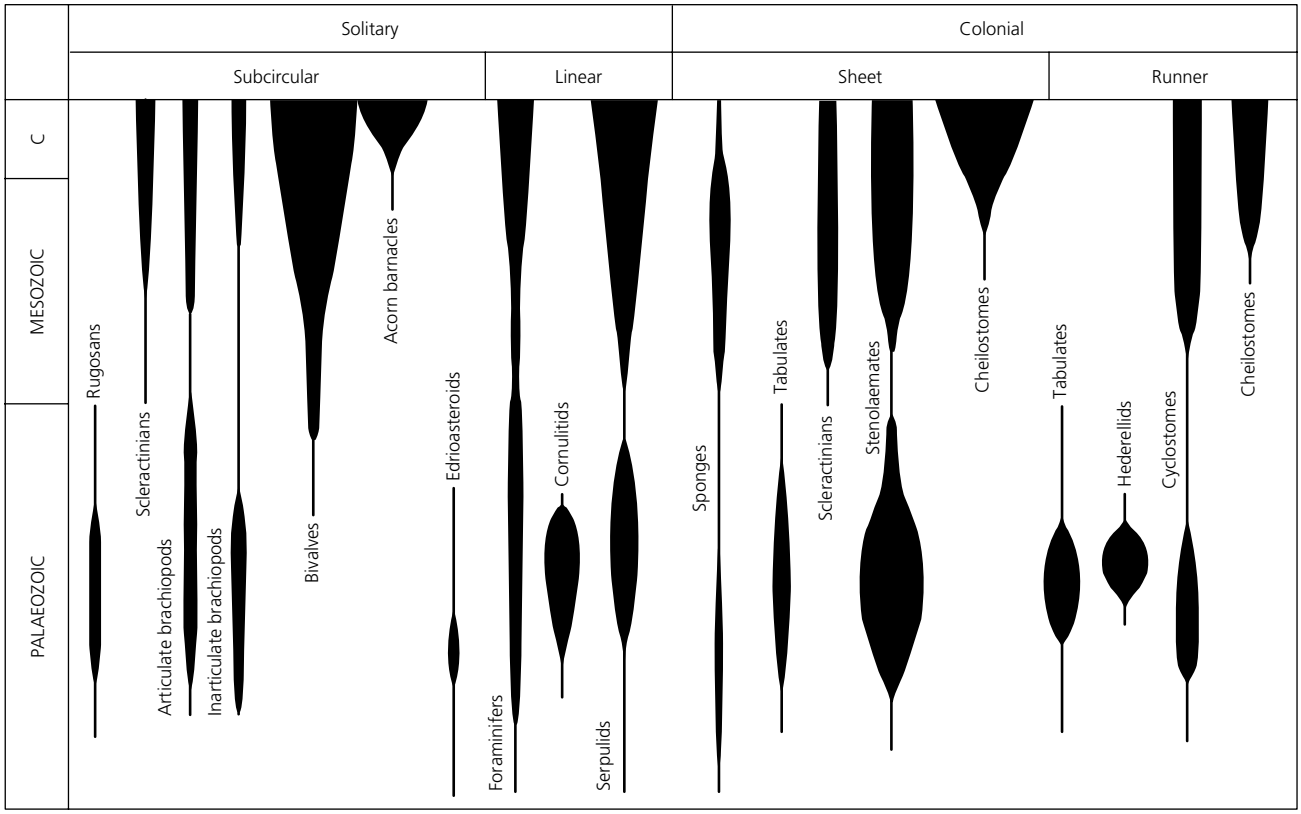


Fig. 4.2.8.1 Stratigraphic distribution and morphological classification of the principal taxonomic groups of encrusting animals represented in epibiont assemblages in the fossil record. Line thickness gives a very approximate indication of the importance of each group in encrusting assemblages. (From Taylor 1990.)

poorly developed planktic food source, or seas with limited hard bottoms that did not support the evolutionary radiation of sessile suspension feeders. Cryptic reef encrusters have been reported from the Lower Cambrian, but in general there is little equivalent to the 'Cambrian Fauna' among epibionts. There are no commensal shell macroborers, and the few known encrusters include phosphatic inarticulate brachiopods and eocrinoids found rarely on arthropods. Most colonial taxa had not yet evolved, but hemichordates, such as uncalcified rhabdopleurids, and perhaps crustoid graptolites colonized some shells. No Cambrian multispecies assemblages of epibionts have been reported.

The Ordovician invertebrate radiations produced many of the familiar Palaeozoic shell encrusters by the Middle Ordovician, including cyclostome and trepostome bryozoans, tabulate corals, craniid brachiopods, cornulitids, and encrusting edrioasteroids (Fig. 4.2.8.2). The shell borers that first occur in the Lower and Middle Ordovician include ctenostome bryozoans, sponges, and commensal annelids.

During the Palaeozoic, epibiont communities experienced gradual faunal turnover. Groups common during the middle Palaeozoic, such as cornulitids, hederellids, edrioasteroids, and auloporid corals, persisted through the Late Devonian extinction into the Carboniferous before disappearing from shells. Encrusting articulate brachiopods, foraminiferans, and boring acrothoracican barnacles first colonized shells in the middle Palaeozoic and gradually became abundant during the upper Palaeozoic. Trepostome bryozoans were one of the most abundant groups of encrusters throughout the Palaeozoic.

The record of epibiont communities during the Palaeozoic–Mesozoic transition is largely unknown, but 'typical' Mesozoic epibiont communities were established at least by the Late Triassic (Taylor and Michalik 1991). Early Mesozoic communities were mixtures of typical Palaeozoic groups, such as spirorbid annelids, craniid brachiopods, acrothoracican barnacles, and rare platyceratid gastropods; reradiations of Palaeozoic groups, such as crinoids, articulate brachiopods (thecideans), and bryozoans (cyclostomes); and new groups, such as bivalves, uncoiled serpulid annelids various foraminiferans, and scleractinian corals. Interestingly, bivalves and uncoiled serpulids, two of the most abundant groups of Mesozoic encrusters, first occur on shells during the Palaeozoic. Gradual changes that occurred during the Mesozoic include the partial replacement of cyclostomes by cheilostome bryozoans, diversification

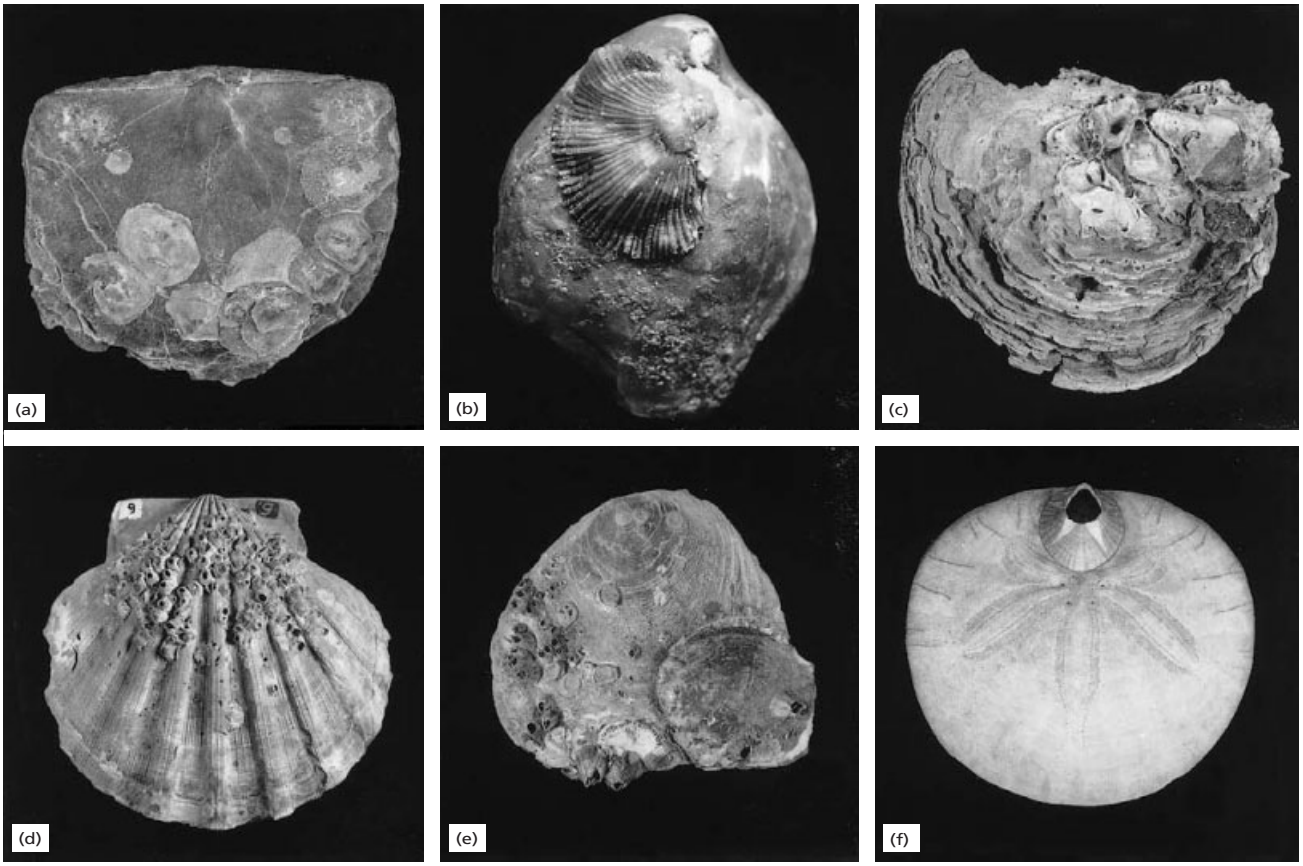


Fig. 4.2.8.2 Examples of epibiont assemblages from various geological times. (a) *Rafinesquina alternata*, Upper Ordovician, Ohio. Assemblage of 11 inarticulate brachiopods (*Petrocrania scabiosa*) along the commissure of the brachial valve. Ecological information preserved in the epibiont assemblage includes probable gregarious settlement (many adjacent inarticulate individuals, some on top of conspecifics), intraspecific competition (distorted outlines of adjacent individuals), and interspecific competition (several *Petrocrania* overgrow a trepostome bryozoan colony (light grey, right of centre), ×1.2. (b) Epibiontic articulate brachiopod *Derbyia* on host brachiopod *Composita*, Curzon Formation, Upper Carboniferous, Kansas, ×2. (c) Flat upper (right) valve of *Exogyra costata*, Navesink Formation, Upper Cretaceous, New Jersey. Epibiont assemblage includes encrusting bivalve *Spondylus echinata*, boring clionid sponge, and boring barnacles, ×0.5. (d) Abundant barnacles on *Chesapecten jeffersonius*, Early Pliocene, Yorktown Formation, Virginia. Epibionts include numerous barnacles and traces of clionid sponge and capulid gastropods (arcuate grooves along lower right margin), ×0.5. (e) Recent *Placuna placenta*, epifaunal recliner on mud, Java Sea. Epibionts include numerous barnacles, and the large oyster *Striostrea*; circular molluscan egg cases are also present, ×0.4. (f) Epibiontic barnacle *Balanus pacificus* on the Recent sand-dollar *Dendraster excentricus*. This specimen illustrates an uncommon instance in which the epibiont selects a live host in response to a unique property of the host. *Balanus* takes advantage of the sand-dollar's vertical life orientation in a turbulent beach environment by settling on the elevated margin. Recent, San Francisco, California, ×0.5.

of bivalve and foraminiferan encrusters, and the appearance of stalked barnacles with calcified plates. Chitinous stalked barnacles have lived on shells, particularly eurypterids, since at least the Silurian.

Cenozoic epibiont communities incorporated three additional groups with abundant individuals, each with predecessors in the Cretaceous. Cheilostome bryozoans continued to replace cyclostomes, and within the cheilostomes simple anascan grade colonies were replaced by ascophorans. Acorn barnacles, which cement directly to the substrate without a stalk, were large and abundant encrusters in productive waters throughout the Cenozoic. They first became abundant in the Palaeogene, but the earliest acorn barnacles are known from a few Cretaceous shoreline environments. Sedentary suspension-feeding calypterid gastropods (e.g. *Crepidula*), which are abundant on shells today, also diversified during the Palaeogene, following a Cretaceous origin.

Epibiont community change

Perhaps the most important contribution that studies of epibiont communities will make to palaeobiology will be

to the understanding of long-term patterns of change within a coherent fossil community type. Epibiont communities from similar environments and hosts, in successive geological periods, can provide data for the analysis of long-term evolutionary patterns and ecological trends. Although our knowledge of evolutionary patterns is primarily qualitative, future studies have the potential to evaluate patterns quantitatively over hundreds of millions of years.

The geological history of epibiont communities suggests that community composition largely reflects the taxonomic history of the constituent taxa, but that taxonomic turnover is more gradual than in other community types. This pattern may reflect in part our incomplete knowledge of epibiont taxonomy, since many encrusters and borers are morphologically simple. The relatively gradual taxonomic turnover probably also reflects the life history characteristics of most epibionts. Epibiont organisms are largely opportunists that settle quickly on a variety of hard substrates and many have large geographical ranges. As suspension-feeding generalists, they were probably less susceptible to extinction than members of other more specialized communities. For example, although the Late Devonian extinction eliminated many brachiopod host species from level-bottom environments, epibiont communities differ little between the Frasnian and Famennian.

Ecological trends

Many of the long-term ecological trends that have been proposed for marine communities can be evaluated on the basis of epibiont communities.

Species richness and diversity

The documented Phanerozoic increase in worldwide species richness has been attributed in large part to the increased number of species within local assemblages. Literature compilations suggest that epibiont communities do not show a general increase in local species richness through time, but display two equally high peaks in the Silurian–Devonian and the Jurassic. Assemblages on non-organic hard substrates show similar peaks. Literature studies, however, may introduce bias because often only the most diverse assemblages are described and sampling is not evenly distributed through time. Epibiont studies of many bulk collections can record abundance and allow trends in ecological diversity to be analysed using the Shannon Index. One such study reveals a gradual decrease in diversity from the Middle Devonian through the Carboniferous (Lescinsky 1997). Peaks in diversity in epibiont communities may reflect high productivity at those times, and support the notion that elevated productivity spurs evolution.

Structural improvement and competitive replacement

Structural improvement among epibionts has been best studied in post-Palaeozoic encrusting bryozoans. Encrusting cyclostomes with simple zooids were gradually replaced by cheilostomes with more highly integrated and specialized zooids. Cheilostomes also developed frontal budding, a colony growth pattern which aids in overgrowth encounters. During the last 100 myr, cheilostomes have consistently overgrown cyclostomes in approximately two-thirds of encounters, and during this interval cheilostomes have become increasingly diverse and abundant (McKinney 1995). It is unclear, however, whether this trend also applies to Palaeozoic bryozoans.

Habitat utilization

Epibionts, like other organisms, have used increasing ecospace during the Phanerozoic, via increased tiering on shells and boring within them. Most early Palaeozoic epibionts are thin and small and encrust strictly on the shell surface. During the upper Palaeozoic, a greater proportion of the cover is composed of erect epibionts such as bryozoans and crinoids (preserved mostly as holdfasts). Many Mesozoic and Cenozoic encrusters are relatively large and elevated above the host shell surface. Acorn barnacles, for example, feed well above the boundary layer near the shell surface. The overall pattern of tiering, however, must be interpreted cautiously because erect species also tend to be the least well preserved, and it is difficult to judge the importance of erect encrusters based primarily on holdfasts. The depth of endobiont borings within shells has also increased, primarily during the Mesozoic (see Section 3.2.2).

Increased energy consumption

The predicted ecological trend of increased energy consumption and biomass among marine organisms appears to apply to epibiont communities. Palaeozoic epibiont communities were composed of very low biomass organisms, with a high proportion of passive suspension feeders. Active suspension feeders and articulate brachiopods with greater biomass became more common in the upper Palaeozoic. Large biomass oysters with high metabolic rates became abundant, and in many cases were the spatially dominant encrusters, during the Mesozoic. Barnacles with high biomass and metabolic rates occurred widely during the Cenozoic.

Increase of skeleton cover

Skeleton cover in epibiont communities shows an increase through time, possibly as the predicted

response to increasing predation pressure. Palaeozoic epibiont communities were dominated by a variety of organisms with exposed soft parts, including trepostome bryozoans, corals, and echinoderms. During the upper Palaeozoic, the proportion of the community area composed of organisms with true external skeletons increased with articulate brachiopods and calcified annelids. Mesozoic and Cenozoic encrusters included thickly shelled bivalves, cheilostome bryozoans with calcified opercula, and acorn barnacles with thick fused plates. The barnacles are a particularly good example of increasingly extensive skeletons, as predicted by escalating predator abilities. Uncalcified stalked Silurian barnacles were followed by calcified stalked Mesozoic forms and Cenozoic acorn barnacles.

References

Kesling, R.V., Hoare, R.D. and Sparks, D.K. (1980) Epizoans of the Middle Devonian brachiopod *Paraspirifer bownockeri:* their relationships to one another and to their host. *Journal of Paleontology* **54**, 1141–1154.

Lescinsky, H.L. (1997) Epibiont communities: recruitment and competition on North American Carboniferous brachiopods. *Journal of Paleontology* **71**, 34–52.

Liddell, W.D. and Brett, C.C. (1982) Skeletal overgrowths among epizoans from the Silurian (Wenlockian) Waldron Shale. *Paleobiology* **8**, 67–78.

McKinney, F.K. (1995) 100 million years of competitive interactions between bryozoan clades: asymmetrical but not escalating. *Biological Journal of the Linnaean Society* **56**, 465–481.

Taylor, P.D. (1990) Encrusters. In: D.E.G. Briggs and P.R. Crowther, eds. *Palaeobiology: a synthesis*, pp. 346–351. Blackwell Scientific Publications, Oxford.

Taylor, P.D. and Michalik, J. (1991) Cyclostome bryozoans from the late Triassic (Rhaetian) of the West Carpathians, Czechoslovakia. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **182**, 285–302.

Ward, M.A. and Thorpe, J.P. (1989) Assessment of space utilization in a subtidal temperate bryozoan community. *Marine Biology* **103**, 215–224.

4.2.9 Fungi in Palaeoecosystems

T.N. TAYLOR and E.L. TAYLOR

Introduction

Despite the importance of fungi in the world today, their role in ancient ecosystems is poorly understood. This reflects a lack of information about their fossil record, and especially how they interacted with other organisms in ancient biotas. This paucity of information is based on the long-held belief that fungi were too fragile to be adequately preserved and the difficulty in recognizing and interpreting diagnostic structures preserved as fossils. In addition, there has been a lack of communication between the palaeobiologists who possess the specimens and the mycologists who have the appropriate expertise. Today there is an increased awareness of the geological occurrence of major fungal groups (Taylor 1993), and a realization that fungal interactions with other organisms can be documented in palaeoecosystems.

Traces preserved in Cambrian reefs and chitinozoan shells may represent the most ancient examples of endolithic fungi, while hyphae and spores from the mid-Silurian demonstrate the earliest unequivocal evidence of terrestrial fungi (Stubblefield and Taylor 1988). However, since these spores and hyphae are known from acid-digested rock samples, nothing is known about how these fungi interacted with other organisms. Most fossil plants occur in the form of impressions and compressions, two preservation types that are generally inadequate to demonstrate fungal interactions. Permineralized specimens, however, hold the potential for providing important information about plant–fungal interactions, since the cells and tissue systems are fossilized. The oldest permineralized fungal specimens come from the famous Rhynie chert site in Aberdeenshire, Scotland (see Section 3.4.5). This Lower Devonian (Pragian) Lagerstätte is characterized as a series of freshwater lakes that were periodically desiccated; the small plants and other organisms (eubacteria, cyanobacteria, algae, and fungi) were fossilized in silica, and thus provide an opportunity to view the many fungal interactions that formed this ancient ecosystem.

Fossil saprobic and parasitic fungi

Within the Rhynie chert are abundant examples of partially decomposed and degraded plant material that reflect the activities of various saprobes. Although hyphae and spores are easily distinguished within plant tissues (Fig. 4.2.9.1a), it is difficult to determine which fungi were responsible for these saprophytic activities. Within the chert are numerous chytridiomycetes, a group of fungi that today includes mainly freshwater saprobes of algae, various microscopic animals, land plants, and other fungi. Since some of these Lower Devonian specimens are morphologically identical to modern forms (Fig. 4.2.9.1b), there is a strong assumption that their nutritional interactions were also similar. This is especially true of *Palaeoblastocladia*, a fossil fungus with the same unique life history as that of some members of the subgenus *Euallomyces*. Other chytrids in the Rhynie chert ecosystem are nutritionally parasites. For example, *Krispiromyces* was parasitic on the charophyte *Palaeonitella*. Normal *Palaeonitella* cells are approx-

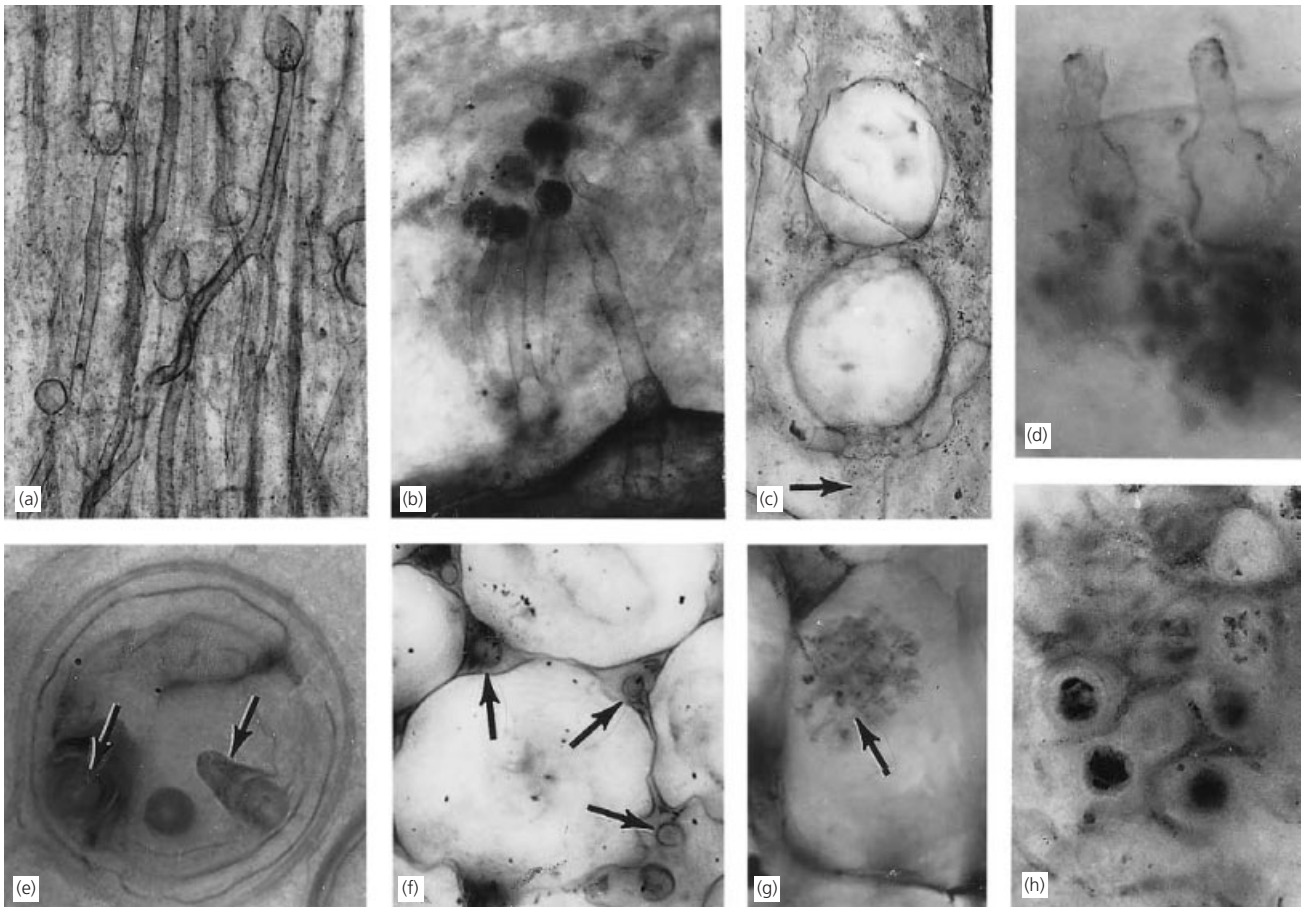


Fig. 4.2.9.1 (a) Hyphae and spores within the tissue of a Rhynie chert plant stem, ×120. (b) Tuft of fungi arising from stem surface, ×200. (c) Two hypertrophied cortical cells of *Palaeonitella*; compare with normal size of axis cells (arrow), ×80. (d) Two chytrid zoosporangia protruding through cell wall; the dark granular material may constitute a host response, ×1000. (e) Rhynie chert chlamydospore with several papillae (arrows) that represent a host response, ×1000. (f) Endomycorrhizal hyphae (arrows) between cortical cells, ×500. (g) Cortical cell with arbuscule (arrow), ×600. (h) Hyphal net of Rhynie chert lichen showing cyanobacterial cell in each of the net lacunae, ×500.

imately 75 µm in diameter; however, those infected by a disc-shaped chytrid thallus exceed 300 µm. These hypertrophied cells (Fig. 4.2.9.1c) represent a host response to the parasite that is identical to that seen in modern fungal–algal interactions. Another host response that occurs in some modern organisms involves the accumulation of starch grains in green plant cells in the presence of certain chytrid parasites. In the Rhynie chert ecosystem the chytrid *Milleromyces* is often found associated with dark bodies that may represent accumulated starch grains (Fig. 4.2.9.1d). Still other Rhynie chert fungi were mycoparasites—fungi that parasitize other fungi. One of the most common hosts are large, thick-walled spores (chlamydospores) probably produced by a zygomycetous fungus. Some of the chytrids that parasitized these spores occurred specifically inside, outside, or between the complex wall layers of the spores. Parasitized spores can be identified by the presence of conical projections that extend into the lumen of the spore (Fig. 4.2.9.1e), and are identical to those found in spores of living fungi. These structures are formed by the protoplast of the spore, which synthesizes new wall material as a defence against the invading parasite. Each of these chlamydospores has the potential to produce hyphae which can become a functioning endomycorrhiza in the community. Thus the reduction in the number of viable spores as a result of mycoparasitism can greatly alter the establishment, size, and viability of succeeding populations in the ecosystem.

Mycorrhizae

Perhaps the most significant event in the establishment of terrestrial ecosystems was the evolution of biotrophic, root-inhabiting fungi, which formed mycorrhizal associations with land plants. These fungal–plant interactions are nearly universal today, occurring in the roots and underground organs of nearly all plants (Fig. 4.2.9.1f). Of

the several types of mycorrhizae encountered today, endomycorrhizae are the most common, occurring in approximately 80% of all vascular plant species. The fungi in these symbioses are responsible for increasing the ability of the plant to capture various nutrients and water, provide protection against soil pathogens and even above-ground herbivores, and increase the physiologically active surface area of the underground system. The reciprocal is that the fungus obtains a source of carbohydrates from the plant. The site for the physiological transfer between the fungus and host cells is a highly branched fungal hypha termed the arbuscule. Endomycorrhizae occur in several Rhynie chert plants and are represented by all phases of the life history of the zygomycetous fossil *Glomites* (Taylor *et al.* 1995). The fossil arbuscules in this association are morphologically identical to those of modern arbuscular mycorrhizae and occur in specialized cortical cells (Fig. 4.2.9.1g). One interesting feature found in the Rhynie chert endomycorrhizal association is the larger percentage of fungal tissue in the fossil host. A logical hypothesis might be that during the initial phases in the evolution of endomycorrhizae, a fungus functioned as a root parasite of the host. As the fungus–host interactions continued to evolve, a physiological equilibrium was established that today represents the modern endomycorrhizal association, and which appears to be more mutualistic than parasitic.

Lichens

Modern lichens represent a symbiosis between a fungus and either a green alga or cyanobacterium, or a combination of these organisms. This association of organisms is responsible in many instances for the initial breakdown of rock that leads to the formation of soil. Because the range of cyanobacteria extends back into the Proterozoic, it might be anticipated that lichens also have a long geological history. However, the earliest unequivocal lichen occurs in the Rhynie chert ecosystem (Taylor *et al.* 1997). *Winfrenatia* consists of a cyanobacterium and a fungus that appears most closely related to a zygomycete. On the upper surface of the thallus are shallow depressions that contain a three-dimensional net-like structure formed of fungal hyphae with each of the spaces occupied by a cyanobacterial cell (Fig. 4.2.9.1h). Different developmental stages within some of the depressions on the lichen thallus suggest that in this association the fungus exerted a level of controlled parasitism over some of the cyanobacterial colonies. For example, some of the depressions contain tightly packed fungal hyphae and a few moribund cyanobacterial cells at the base of the depression, suggesting that the fungus completely parasitized its photosynthetic partner. In others, however, there appears to be a consistent relationship between the fungus and the cyanobacterial cells, indicating a mutualistic association between the two partners. In this unique symbiosis the benefit to the cyanobacterium may have been the opportunity to colonize new niches, as well as providing protection from invertebrate herbivory.

Major fungal groups through geological time

The major groups of fungi known from the Rhynie chert ecosystem are the Chytridiomycota (zoosporic fungi), Zygomycota, and the Ascomycota (sac fungi). By Lower Devonian time these groups appear to be well diversified, based on thallus morphology and the degree of interaction with other organisms. The zoosporic fungi may have been the principal saprobes at this time, while the zygomycetes already had the ability to form mutualistic symbioses with plants and cyanobacteria.

Although structures suggestive of the Ascomycota have been reported as early as the mid-Silurian (Sherwood-Pike and Gray 1985), the geological history of the group has been especially difficult to decipher (Taylor 1994). Several spore-producing bodies that appear in the Carboniferous mimic the ascocarps of modern forms, but similar-looking structures are known in other groups of fungi. By Cretaceous time there are excellent examples of leaf-inhabiting fungi which are morphologically identical to many modern ascomycetes. Although the hosts are now extinct, the life history of many of the fossils exactly mirrors a number of epiphyllous, parasitic forms today. A recent discovery indicates that ascomycetes were also present in the Lower Devonian Rhynie chert (Taylor *et al.* 1999). These fungi occur in the cortical tissues of at least one of the Rhynie chert plants and, like some of their modern counterparts, may have been plant parasites. The ascomycete fruiting body is flask-shaped and contains elongate asci, each with numerous bicelled ascospores.

The earliest evidence of basidiomycetes occurs as wood rot in the Upper Devonian progymnosperm *Callixylon*, based on degradation patterns on the tracheid walls (Stubblefield and Taylor 1988); clamp connections, a key diagnostic feature of basidiomycetes, are first recorded in the Carboniferous. Spindle-shaped pockets that constitute a specific symptom of certain wood rotting fungi are known from several Permian gy nosperm woods. This symptom is identical to that in modern woods. Equally fascinating is the fact that the pattern of cellulose and lignin degradation is identical, which provides compelling evidence that the enzymatic patterns of these ancient saprobes evolved very early and have apparently remained unchanged until today.

Fungal–animal interactions

Fungi are also variously associated with animals in modern ecosystems, and although rare in the fossil

record, such interactions have been documented. The earliest example involves what are interpreted as faecal pellets of Silurian age, composed entirely of bits of fungal hyphae (Sherwood-Pike and Gray 1985). Because the Rhynie chert also contains numerous arthropods, it is anticipated that this site will ultimately provide some of the first direct evidence of animal–fungal interactions. Other fossil examples of fungal–animal interactions include fungi functioning as saprobes on animal parts preserved in amber (Stubblefield and Taylor 1988) and as obligate symbionts in Triassic arthropods (White and Taylor 1989).

There is abundant evidence for the presence of well-preserved fungi in the fossil record and an increasing awareness of their importance through geological time. Recording their presence not only provides critical information on the minimum divergence time for major fungal groups, based on molecular data, but also offers the only source of information about the many levels of interactions between fungi and other organisms in the palaeoecosystem.

References

Sherwood-Pike, M.A. and Gray, J. (1985) Silurian fungal remains: probable records of the class Ascomycetes. *Lethaia* **18**, 1–20.

Stubblefield, S.P. and Taylor, T.N. (1988) Tansley Review no. 12. Recent advances in paleomycology. *New Phytologist* **108**, 3–25.

Taylor, T.N. (1993) Fungi. In: M.J. Benton, ed. *The Fossil Record 2*, pp. 9–13. Chapman and Hall, London.

Taylor, T.N. (1994) The fossil history of Ascomycetes. In: D.L. Hawksworth, ed. *Ascomycete systematics: problems and perspectives in the nineties*, pp. 167–174. NATO ASI Series A: Life Sciences, no. 269. Plenum Press, New York.

Taylor, T.N., Remy, W., Hass, H. and Kerp, H. (1995) Fossil arbuscular mycorrhizae from the Early Devonian. *Mycologia* **87**, 560–573.

Taylor, T.N., Hass, H. and Kerp, H. (1997) A cyanolichen from the Lower Devonian Rhynie chert. *American Journal of Botany* **84**, 992–1004.

Taylor, T.N., Hass, H. and Kerp, H. (1999) The oldest fossil ascomycetes. *Nature* **399**, 648.

White, J.F. Jr and Taylor, T.N. (1989) A trichomycete-like fungus from the Triassic of Antarctica. *Mycologia* **81**, 643–646.

4.3 Fossils as Environmental Indicators

4.3.1 Taphonomic Evidence

M.V.H. WILSON

Introduction

The study of taphonomy—the field of inquiry into the biological and physical factors affecting fossil organisms between their death and their burial—has enormous potential to contribute to the reconstruction of palaeoenvironments (see Sections 3.3 and 3.4). In the past, palaeontologists tended to focus mainly on what can be thought of as 'taphonomic loss', i.e. the negative effects of taphonomic agents on the information preserved in the fossil record. Examples of loss of information include mixing of faunas in death assemblages, sorting and damaging of hard parts, and loss of temporal resolution through reworking and non-preservation. Such losses interfere with research goals such as community reconstruction and biostratigraphic correlation, and the researcher will typically attempt to minimize them or at least to take them into account. For example, to compensate for selective preservation, biostratigraphers and palaeoecologists intentionally sample a range of lithologies and localities.

The recent emphasis on taphonomic evidence in palaeoenvironmental reconstruction can be thought of as a focus on 'taphonomic gain' (Wilson 1988), so called because taphonomic agents not only reduce certain kinds of palaeontological information, but also increase other information by leaving characteristic evidence or signatures. Recognition of these signatures enables the careful observer to learn much about the conditions of death, decay, transportation, deposition, and preservation, making a useful contribution to fields such as palaeoecology and sedimentology.

Principles

The early North American history of taphonomy emphasized the recognition of taphonomic loss (Wilson 1988)

and often futile attempts to reconstruct life assemblages, whereas in Europe (Cadée 1991) the focus was more commonly on the observation of modern taphonomic processes (Aktuopaläontologie), along with a search for comparable fossil examples, and on the interpretation of exceptional fossil deposits (Fossil-Lagerstätten). Taphonomy also has a strong tradition in archaeology where, perhaps understandably, taphonomic gain through recognition of taphonomic signatures has been a fruitful avenue of investigation.

There are two main ways in which taphonomic gain can be realized by palaeontologists. The first and more specific involves the recognition of the effects of particular taphonomic agents through their taphonomic signatures; the second involves the recognition of suites of co-occurring taphonomic characteristics, or taphofacies (Speyer and Brett 1986).

Identification of the particular taphonomic agent responsible for a taphonomic signature requires uniformitarian extrapolations (Wilson 1988). Most often these extrapolations are from the Recent to the past, either from actuopalaeontological observations of natural phenomena, or from experiments, and are, of course, of varying reliability. Taphonomic agents can be either physical (e.g. currents, temperature, volcanic eruption) or biological (e.g. predator, scavenger, decomposer). Uniformitarian extrapolations are usually more reliable when they deal with physical agents than they are when they deal with biological agents. All of these can be the subject of actualistic observations (e.g. studies on modern, naturally occurring death assemblages and their causes; observations on feeding behaviour and digestive residues in living predators) or experimental investigation (e.g. experiments on implosion of nautiloid shells in deep water; and studies in flow tanks of transportation, sorting, and deposition of skeletal remains).

Taphofacies can be recognized without necessarily drawing conclusions about particular causes (although they become much more informative when their taphonomic agents are understood). Taphofacies can be studied in a taxon-specific context, or in a multidisciplinary, comparative one. They can aid in the recognition of geologically relevant palaeoenvironments within a single formation, or of temporal change in palaeoenvironments at a single location. An evolutionary application of a similar concept was advocated by Behrensmeyer *et al.* (1992), who argued that changes, over geological time, in terrestrial communities must be studied within taphonomically similar contexts, reflecting similar environments and preservational biases.

Both taphonomic signatures and taphofacies can be extremely powerful tools, able to reveal subtle changes in the environment, even in the absence of obvious differences in sedimentology or taxonomic composition of an assemblage. However, like other palaeontological evidence, and partly because of its extreme sensitivity, taphonomic evidence in typical palaeontological samples is particularly subject to time-averaging and loss of temporal resolution (Wilson and Barton 1996) (see Section 3.2.7). Samples may be time-averaged prior to preservation as fossils, owing to such causes as tiering of the living organisms or reworking of their remains. Time-averaging can also occur in samples if collecting techniques have lacked precision. Possible situations with near-optimal temporal resolution include mass-mortality layers, although even in such cases the taphonomic agents may have been active over weeks or months.

Applications

There are numerous examples of the application of taphonomic gain to palaeoecology; only some examples can be highlighted here, with some attempt at taxonomic and geological breadth. Taphonomic agents can usefully be divided into physical and biological ones, with taphofacies briefly treated at the end.

Physical factors include energy of the environment, pressure, and chemistry. It will be immediately obvious that the energy of the aerial or aquatic environment is of outstanding importance in determining the taphonomic characteristics of assemblages. Winds, currents, waves, and water turbulence all have major impacts on the fossilization process, leading to such signatures as fossils sorted by size and by taxon (e.g. land plant remains deposited in lakes), invertebrate and vertebrate skeletons orientated linearly by waves or currents (e.g. crinoid stem fragments, fish skeletons in over-bank ponds) (Fig. 4.3.1.1), and skeletons fragmented and abraded by moving water and sediment (see Section 3.2.6). Other physical factors may seem less obvious but are no less important. Water pressure can cause implosion of cephalopod shells at depth, and recognition of this taphonomic signature allows conclusions about the depth of the depositional environment. An interplay between depth and pressure determines whether swim-bladder-equipped teleost fishes (and other gas-filled organisms) float after death, or sink directly to the bottom (Elder and Smith 1988). The alternative fates can be recognized by characteristic patterns of bone loss from the skeletons. Chemical factors include anoxia (of the water or the sediment), which can retard certain kinds of decay and prevent scavenging and reworking.

Biological agents are equally important, though often limited in their activity by physical factors as noted above. Obvious examples are predators that have inflicted distinctive damage to prey species (e.g. presumed mosasaur bite marks in ammonite shells,

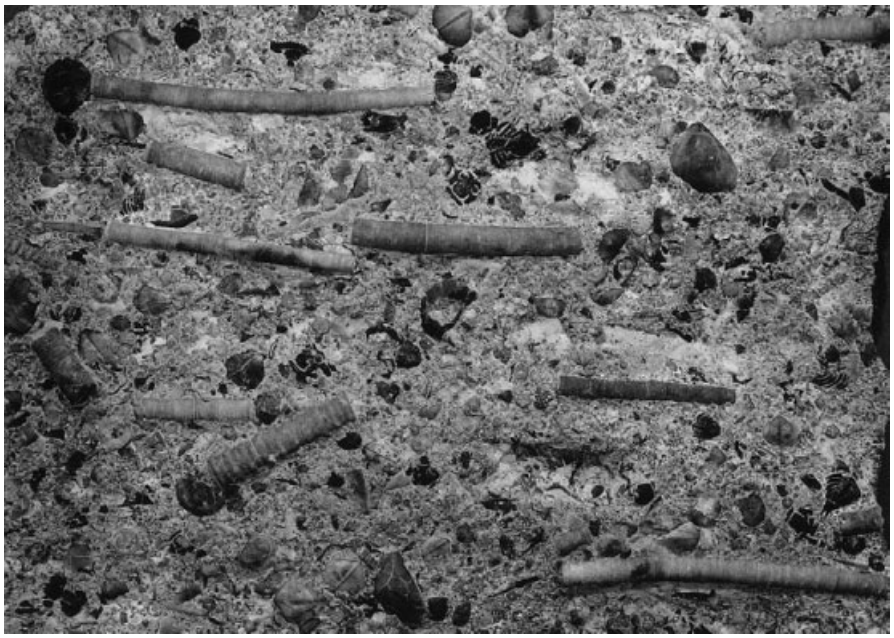


Fig. 4.3.1.1 Crinoid column fragments aligned by water movement in the Lower Silurian Jupiter Formation of Anticosti Island, Canada, ×0.6 (Specimen photographed courtesy of Dr B.D.E. Chatterton.)

Fig. 4.3.1.2 An Eocene teleostean fish (*Amyzon aggregatum*) from Horsefly, British Columbia, Canada, showing a moderate amount of scavenger disturbance of skull bones, ×1.2. (From Wilson and Barton 1996.)

although limpets have also been proposed as agents for this damage), or left their teeth embedded in fossilized prey specimens (dinosaur examples are numerous). Faecal remains, preserved as coprolites, can reveal much about the biology of the predator, and even when the predator is difficult to identify, they are an important and often recognizable source of fossil remains. The activities of scavengers can also sometimes be identified, though the particular scavenger might remain unknown (e.g. studies of scavenged fish skeletons by Elder and Smith 1988) (Fig. 4.3.1.2).

Taphofacies analysis is making increasing contributions to palaeoecological reconstruction. Studies on trilobites (e.g. Speyer and Brett 1986) have demonstrated its utility in a Palaeozoic marine context, where it reveals patterns of associated taphonomic signatures reflecting such environmental factors as rates of sedimentation and bathymetry. Taphonomic characterization of deposits in which terrestrial organisms are preserved (Behrensmeyer *et al*. 1992) shows promise as a method for identifying similar palaeoenvironments and allowing for studies of community evolution within similar taphofacies. In lacustrine deposits, taphonomic characteristics together with relative abundances of plants, insects, and fishes allow division of assemblages into broad palaeoenvironmental categories, often with a strong nearshore–offshore trend. Faunal and floral comparisons of different geological ages and of different geographical locations will yield meaningful results only if like palaeoenvironments are compared.

Conclusion

Study of the taphonomic characteristics of fossil deposits can be a powerful tool in palaeoecology, but one that has been exploited to its full potential all too seldom. Recognition of the taphonomic signatures of physical and biological agents, and more generally the classification of fossil deposits into taphofacies, are the main ways in which taphonomic gain has been realized to date. The taphonomist should of course be aware of the often questionable uniformitarian assumptions involved in taphonomic inference, as well as the potential for taphonomic signatures to be temporally averaged and otherwise obscured, as indeed with any other palaeontological data. Nevertheless, taphonomic analysis should make an increasingly positive contribution to palaeoecological reconstruction in the years ahead.

References

Behrensmeyer, A.K., Damuth, J.D., DiMichele, W.A., Potts, R., Sues, H.-D. and Wing, S.L., eds. (1992) *Terrestrial ecosystems through time: evolutionary paleoecology of terrestrial plants and animals*. University of Chicago Press, Chicago.

Cadée, G.C. (1991) The history of taphonomy. In: S.K. Donovan, ed. *The processes of fossilization*, pp. 3–21. Belhaven Press, London.

Elder, R.L. and Smith, G.R. (1988) Fish taphonomy and environmental inference in palaeolimnology. *Palaeogeography, Palaeoclimatology, Palaeoecology* **62**, 577–592.

Speyer, S.E. and Brett, C.E. (1986) Trilobite taphonomy and Middle Devonian taphofacies. *Palaios* **1**, 312–327.

Wilson, M.V.H. (1988) Taphonomic processes: information loss and information gain. *Geoscience Canada* **15**, 131–148.

Wilson, M.V.H. and Barton, D.G. (1996) Seven centuries of taphonomic variation in Eocene freshwater fishes preserved in varves: paleoenvironments and temporal averaging. *Paleobiology* **22**, 535–542.

4.3.2 Oxygen in the Ocean

W. OSCHMANN

Introduction

Following the anoxic conditions of the Archaean, levels of free oxygen in the surface waters of the oceans have been sufficiently high for about 2.3 billion years to support an oxygen-based respiratory mode of life. In these environments heterotrophic eukaryotes, including metazoans, evolved and adapted to an obligate aerobic metabolism (see Section 1.1). By late Proterozoic times the concentration of oxygen in the atmosphere was sufficiently high to oxygenate the oceans at depth by current-induced vertical turnover of water masses. The Phanerozoic can therefore be regarded as the oxygenated period of Earth history. However, particular combinations of climatic, oceanographic, and geographical factors have caused widespread oxygen depletion or anoxia during certain periods of the Phanerozoic (e.g. Ordovician through Devonian, Jurassic, and Cretaceous). Subtropical west-coast trade wind systems, periods of global greenhouse, global sea-level rise, and semi-enclosed basins with estuarine circulation systems either promote increased rates of primary production or favour reduced rates of oceanic turnover. Diminished oxygen supply to deeper water and rapid oxygen consumption result in depletion. Specific environments (e.g. silled basins, upwelling systems, and eutrophic shelf areas) commonly are characterized by density–stratification (thermocline and/or halocline) of the water column with temporary to permanent oxygen depletion in bottom waters (e.g. Oschmann 1988; Wignall 1994). Many organisms within these environments developed particular adaptations to maintain an aerobic metabolism where oxygen is limited.

Adaptive strategies of benthic organisms in marine oxygen-controlled environments

Physiological and morphological adaptations

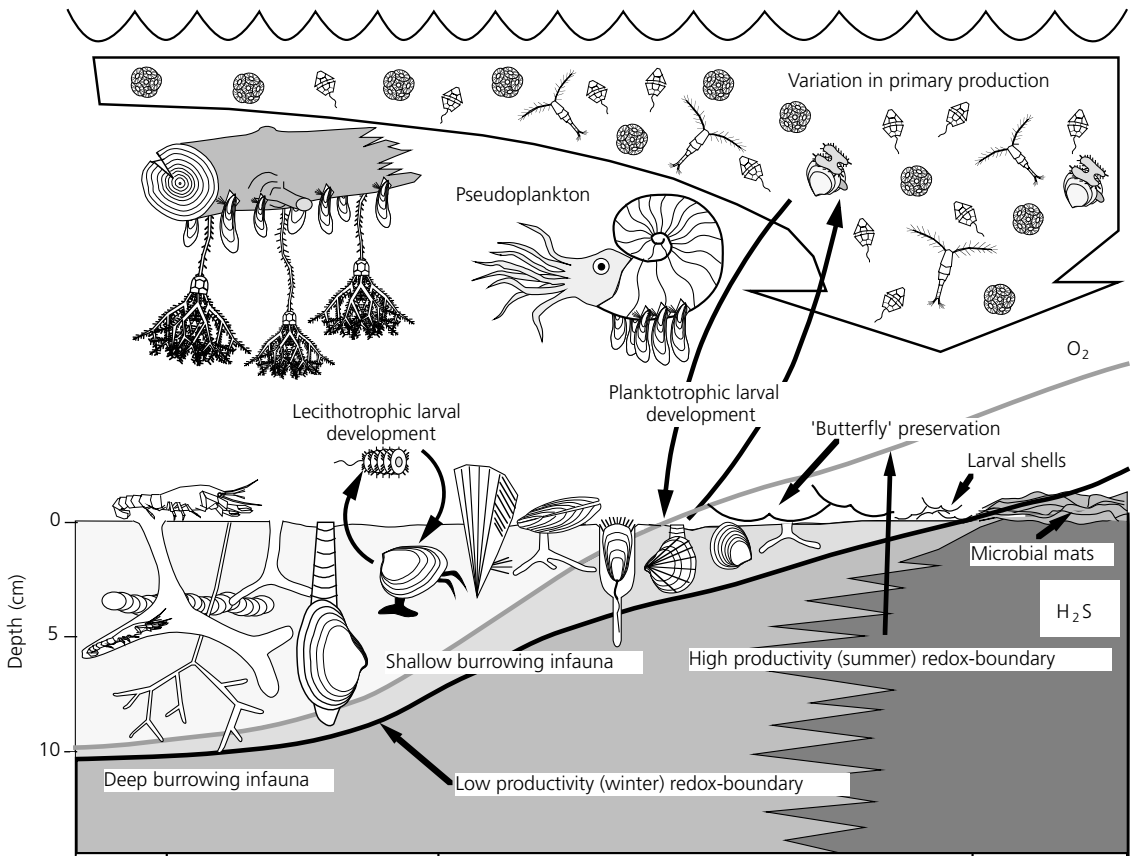
Many organisms which inhabit oxygen-depleted environments have to struggle with conditions that are far from optimal. A common strategy is to reduce the rate of metabolism and thus the uptake of oxygen. As a result, growth rates are much lower and individuals may become dwarfs. Some groups of organisms are able to switch, for limited periods of time (days to weeks), to a modified metabolic pathway (the succinate pathway) which can be maintained without oxygen. Efficient blood circulatory systems (e.g. in many polychaetes) and effective oxygen-binding pigments (e.g. in the 'blood arks' *Anadara* and *Scapharca*: bivalve family Arcidae) optimize uptake of the limited oxygen resources. A change in body shape (e.g. in 'flat clams' or thread-like 'worms') supports absorption and diffusion of oxygen via surface tissues, a habit which is also inferred in some fossil bivalve groups (e.g. Triassic monotids, halobiids). In many respects bivalves and polychaetes are particularly well adapted to periods of oxygen depletion (Oschmann 1994).

Another physiological adaptation is increased tolerance to toxic H_2S. Gaseous H_2S is present within most oxygen-depleted environments where sulphate-reducing bacteria degrade organic matter. H_2S is an

extremely potent neurotoxin and causes cessation of pulmonary function by blocking cytochrome *c* and oxygen-binding pigments. Certain H_2S-binding and -transporting pigments in blood fluid allow some organisms to survive temporarily in the H_2S biome. Various organisms have developed a mutualistic relationship with endosymbiotic, chemolithoautotrophic bacteria (endobenthic lucinid and solemyid bivalves, for example, which occur in black shales at least from Jurassic times onwards: Oschmann 1994). The bacteria form glucose and starch by oxidizing H_2S pumped by the bivalves from the reduction zone. Oxygen is supplied from the bottom water. Part of the glucose and starch provided by the bacteria is consumed by the bivalves for oxidative metabolism. The bacteria oxidize H_2S and thus prevent poisoning of the bivalves.

Synchronization of life cycles with oxygen fluctuation cycles

The seasonal cycle generates the strongest changes of temperature, light, wind and water circulation, nutrition supply, and oxygen availability on Earth. Many organisms have evolved strategies to cope with these fluctuations. Reproductive cycles are particularly susceptible to seasonal oxygen depletion. In the holo-benthic life cycle, direct or lecithotrophic larval development takes place within the bottom water (Fig. 4.3.2.1). Larvae and adults live more or less in the same environment, and both die in the event of anoxia. Typical examples are nuculid bivalves, which can survive limited periods of oxygen depletion, but rapidly disappear when the environment becomes temporarily anoxic (e.g. Oschmann 1994).



	Aerobic	Dysaerobic			Anaerobic
ml O_2 / l H_2O	>2	Moderate 2–1	Severe 1–0.5	Extreme 0.5–0	0 ml
	Aerobic	Poikiloaerobic			Anaerobic
mmol O_2 / l H_2O	>0.1	Moderate summer: <0.1	Severe winter: <0.1 summer: <0.05	Extreme winter: <0.1 summer: <0.02	<0.01

Fig. 4.3.2.1 Oxygen-related biofacies zonation.

The pelago-benthic life cycle involves a planktotrophic larval stage that takes place in surface waters and may last several weeks to months (Fig. 4.3.2.1). The larvae are therefore unaffected by harmful conditions in bottom waters, unlike the adults, which may be killed by the onset of bottom anoxia. In fossil environments, this is reflected in regular occurrences of 'butterfly preservation' of infaunal bivalves in black shales (where the shells have not been disturbed after death). The occurrence of larval and small juvenile shells on the bedding planes of various Mesozoic black shales (e.g. Toarcian Posidonia Shale, Kimmeridge Clay) shows where larval swarms tried to resettle, but failed due to extended periods of anoxia (e.g. Oschmann 1994). The pelago-benthic life cycle requires an early reproductive age (i.e. sexual maturity within 1 year) and a mechanism for triggering the shedding of gametes in response to decreasing oxygen. This cycle is also a prerequisite for the well-known pseudoplanktic life style, which is evidenced, for example, by the attachment of bivalves and other taxa to driftwood and ammonites in Toarcian black shales (e.g. Oschmann 1994; Wignall 1994).

An extended, teleplanic larval stage is characteristic of various Recent bivalves and gastropods. The duration of this planktotrophic larval stage can be up to 18 months and it allows species to survive prolonged phases of anoxia. A further extension of the larval stage may result in a progenetic holo-pelagic life cycle. The Panthalassa- and Tethyan-wide distribution of Triassic and Jurassic monotids, halobiids, and posidoniids indicates a teleplanic larval development or a holo-pelagic life cycle allowing wide dispersal.

Classification of modern and ancient oxygen-controlled environments

The classic model of oxygen-deficient marine environments (Rhoads and Morse 1971) distinguished aerobic, dysaerobic, and anaerobic biofacies where conditions were stable in the longer term. This classification is used, with slight modification, in most studies of ancient oxygen-controlled environments (Fig. 4.3.2.1) (e.g. Tyson and Pearson 1991; Wignall 1994). Oxygen values are given as ml O_2/l H_2O, but are better expressed as mmol O_2/l H_2O, as this relationship is not pressure-related and remains valid in deeper water. Observations in modern environments show that oxygen fluctuations are usually very dynamic. In many cases, a distinct seasonal cyclicity is prominent. This is the basis for an alternative classification incorporating seasonal effects (Fig. 4.3.2.1) (Oschmann 1994).

The aerobic biofacies is characterized by epifauna and shallow- as well as deep-burrowing infauna, e.g. crustaceans and molluscs (mainly heterodont bivalves). Such taxa usually live above the redox-boundary and are preserved occasionally in life position. The penetration depth of trace fossils and burrowing bivalves can be used to estimate the depth of the redox-boundary within the substrate.

Within the dysaerobic/poikiloaerobic biofacies, deeply burrowing bivalves and trace fossils are absent. This reflects the shallow position of the redox-boundary within the substrate. These biofacies are commonly characterized by a remarkably reduced diversity. The fauna consists mainly of shallow burrowers (e.g. *Lingula*, small strombid gastropods, and small heterodont bivalves) and some recliners adapted to soft substrates. In severe and particularly in extreme dysaerobic/poikiloaerobic biofacies, monospecific associations of epifaunal or infaunal bivalves dominate. 'Butterfly preservation' of infaunal bivalves is common and records the migration of the redox-boundary up into the water column. Most taxa of this biofacies have planktotrophic larvae, which develop within the surface waters. The sporadic occurrence of larval shells indicates failed larval spatfalls during unfavourable conditions.

The anaerobic biofacies is characterized by microlaminated, undisturbed sediments with relatively high proportions of organic matter (TOC—total organic carbon). Occasionally, microbial mats occur that may have been formed by sulphate-reducing or sulphide-oxidizing bacteria (e.g. Oschmann 2000). Shells of macroorganisms that lived as pseudoplankton attached to tree trunks and ammonites in the surface waters may also be preserved. Their presence is not restricted to the anaerobic biofacies but their preservational potential is much higher there.

References

Oschmann, W. (1988) Kimmeridge Clay sedimentation—a new cyclic model. *Palaeogeography, Palaeoclimatology, Palaeoecology* **65**, 217–251.

Oschmann, W. (1994) Adaptive pathways of marine benthic organisms in oxygen-controlled environments. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **191**, 393–444.

Oschmann, W. (2000) Microbes and black shales. In: R. Riding and S.M. Awramik, eds. *Microbial sediments*, pp. 137–148. Springer-Verlag, Heidelberg.

Rhoads, D.C. and Morse, I.W. (1971) Evolutionary and ecological significance of oxygen-deficient marine basins. *Lethaia* **4**, 413–428.

Tyson, R.V. and Pearson, T.H., eds. (1991) *Modern and ancient continental shelf anoxia*. Geological Society Special Publication, no. 58.

Wignall, P. (1994) Black shales. *Oxford Monographs in Geology and Geophysics* **30**, 1–127.

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4.3.3 Carbon Isotopes in Plants

D.J. BEERLING

Introduction

The stable carbon isotopes of carbon, ^{12}C and ^{13}C, have always been present in the atmosphere, with the majority in the ^{12}C form (≈87%), giving a molar ratio between the two of 0.01115 (for 1988). Generally the $^{13}C/^{12}C$ ratio of fossil material, and of CO_2 in air samples, is expressed as a deviation from the molar ratio in the standard, taken as the fossil Pee Dee Belemnite formation (Upper Cretaceous) in South Carolina (denoted PDB):

$$\delta^{13}C_p = \frac{^{13}C/^{12}C_{sample}}{^{13}C/^{12}C_{standard}} - 1 \quad (1)$$

The $^{13}C/^{12}C$ ratio of the PDB standard has traditionally been taken as 0.01124, but recent analyses suggest that 0.01118 is more appropriate (Farquhar and Lloyd 1993). The deviation from the PDB standard is usually presented as 'parts per mil' (=×10^3 or ‰) using the δ notation. Note that ‰ is not a unit and δ is dimensionless. In equation (1) therefore, $\delta^{13}C_p$ is the deviation of the samples relative to the standard.

During the process of photosynthesis, discrimination against the heavier isotope, ^{13}C, occurs so that the carbon isotope composition of plants is usually negative relative to the PDB standard (cf. Table 4.3.3.1). The extent of biological discrimination (Δ) against ^{13}C can be calculated when the isotopic composition of the source CO_2 is known, by:

$$\Delta = \frac{\delta^{13}C_a - \delta^{13}C_p}{\left(1 + \frac{\delta^{13}C_p}{1000}\right)} \quad (2)$$

where $\delta^{13}C_a$ is the proportional deviation from the PDB standard of atmospheric CO_2 and $\delta^{13}C_p$ is the proportional deviation from the PDB standard of the plant sample. Discrimination is therefore independent of $\delta^{13}C_a$ and directly expresses the consequences of biological processes. From equations (1) and (2), plant material with a molar abundance ratio ($^{13}C/^{12}C$) of 0.01095 has a $\delta^{13}C_p$ value of –25.73‰ (equation 1) (using the traditional PDB standard), and a discrimination value (equation 2), with $\delta^{13}C_a$=–7.7‰, of 18.506‰.

Measurements of stable carbon isotope composition of fossilized leaves, fruits, seeds, and pollen provide information on the likely photosynthetic pathway; isotopic composition of the source CO_2 fixed by leaves during CO_2 assimilation; and information on the forcing of plant growth by past climates (Beerling 1997). The $\delta^{13}C_p$ values of terrestrial vegetation also influence the $\delta^{13}C_p$ of soil organic matter, and the teeth and bones of herbivorous mammals (see Beerling 1997 and references therein).

Table 4.3.3.1 Typical values for molar abundance ratio ($^{13}C/^{12}C$), $\delta^{13}C$, and isotopic discrimination (Δ) of plants. (From Jones 1992.)

Plant group	$^{13}C/^{12}C$	$\delta^{13}C$ (‰)	Δ (‰)
C_3 plant material	0.01085–0.01102	–20 to –35	13 to 28
C_4 plant material	0.01107–0.01116	–7 to –15	–1 to 7
CAM plant material	0.01099–0.01112	–10 to –22	2 to 15

Diagenetic effects

Burial of organic matter over time leads to the selective removal of its constituent components such as hemicellulose, lignin, and cellulose. Because each component has a different $\delta^{13}C$ value, this has the potential to alter the isotopic composition of the bulk organic matter during fossilization, due to differential preservation of its organic constituents. Consequently, plant cuticles have more negative values than bulk organic carbon or wood. However, the impact of diagenetic modification on studies of fossil plant $\delta^{13}C_p$ may be overestimated, since isolating a specific compound (e.g. cellulose), or even molecule, from the fossils overcomes some of these concerns. In addition, provided that comparisons of $\delta^{13}C_p$ values are made between materials of a similar age, rather than with modern (unfossilized) material, it is often assumed that changes in the $\delta^{13}C_p$ of fossil plant material through a section represent a response by the plant to some changing feature of the environment, rather than diagenesis.

Photosynthetic pathway

The photosynthetic pathway of terrestrial plants exerts a strong influence on the isotopic composition of the resulting organic matter. Plants which employ the C_3 photosynthetic pathway use the enzyme ribulose 1,5-bisphosphate carboxylase/oxygenase (rubisco) for the initial carboxylation (to form the three-carbon-molecule phosphoglyceric acid) and have more negative $\delta^{13}C_p$ values than C_4 plants, which use phosphoenolpyruvate (PEP) carboxylase (to form the four-carbon-molecule oxaloacetic acid) for the initial carboxylation. The difference arises because PEP carboxylase discriminates much less against ^{13}C than rubisco. A third group of plants, typically succulents, use crassulacean acid metabolism (CAM); these plants represent intermediates since they assimilate only small

amounts of CO_2 during the day via the C_3 pathway and operate in CAM mode with the C_4 pathway at night, when the stomata tend to remain closed (Vogel 1993). The overlap in the $\delta^{13}C_p$ ranges (Table 4.3.3.1) precludes absolute identification of the photosynthetic pathway, without additional contextual information.

Carbon isotope signatures of past global change in fossils

An improved understanding of the environmental and biological controls on $\delta^{13}C_p$ within C_3 plants has extended the application of stable carbon isotope work in palaeobiology to enable its use as a sensitive 'tool' to detect changes in the global carbon cycle, climate, and vegetation activity (Farquhar and Lloyd 1993). A simplified model defines the interrelationship between $\delta^{13}C_p$ and leaf gas exchange in C_3 plants:

$$\delta^{13}C_p = \delta^{13}C_a - a - (b - a) \times \frac{p_i}{p_a} \quad (3)$$

where a is the isotopic discrimination against $^{13}CO_2$ in free air and during diffusion through the stomatal pores (4.4‰), b is the fractionation associated with rubisco (27‰), p_i is the CO_2 partial pressure in the substomatal cavity, and p_a is the CO_2 partial pressure outside the leaf (Farquhar and Lloyd 1993). The p_i/p_a ratio is controlled largely by environmental effects influencing photosynthetic CO_2 fixation and stomatal activity. Modelling work has shown that it is possible to reproduce general trends in the $\delta^{13}C_p$ of plant organic matter over the past 400 million years using equation (3) and information on leaf gas exchange processes (Beerling and Woodward 1997) (Fig. 4.3.3.1). This implies that our present-day understanding of processes controlling plant isotopic composition are applicable for investigating plant activity in the distant past.

Given that a and b are constant, equation (3) shows that $\delta^{13}C_p$ is sensitive to changes in both $\delta^{13}C_a$ and the p_i/p_a ratio. Measurements of $\delta^{13}C_p$ of fossilized organic matter can be used to test whether large variations in $\delta^{13}C_a$ occurred during episodes of past global change, assuming that any changes in $\delta^{13}C_p$ exceed environmental effects on the p_i/p_a ratio. Since atmospheric CO_2 is well-mixed globally, marked $\delta^{13}C_a$ excursions may also be recorded in the isotopic composition of organic carbon of land plants worldwide with the largely undeveloped potential for correlating terrestrial and marine sequences and improving interpretation of coupled ocean–atmosphere responses in the geological past.

C_4 plants and $\delta^{13}C_a$ reconstructions from fossils

A similar model of isotopic fractionation developed for C_4 plants (see Farquhar and Lloyd 1993 for an overview) shows that the isotopic composition of C_4 plant materials is related to that of the source CO_2. The model can be simplified to:

$$\delta^{13}C_a = \delta^{13}C_p + \Delta \quad (4)$$

Since Δ is a characteristic value for a given plant species, determination of Δ for a particular extant C_4 species present in the fossil record enables, theoretically, $\delta^{13}C_a$ to be calculated from measurements of $\delta^{13}C_p$. Ecophysiological work on a range of C_4 grasses suggests that physiological variations in Δ can occur, limiting the purported high-precision nature of this approach.

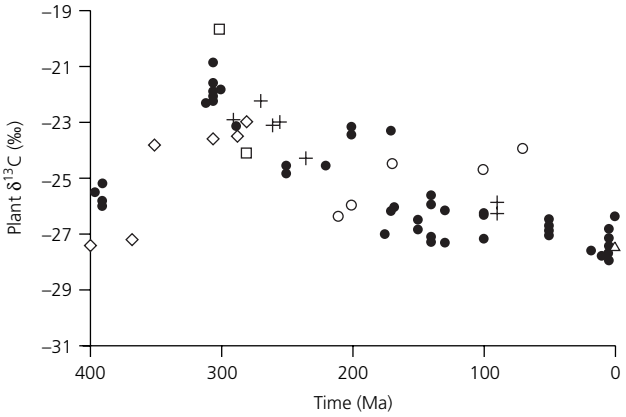

Fig. 4.3.3.1 Changes in the predicted and measured stable isotopic composition $\delta^{13}C$ (‰) of a variety of different sources of terrestrial organic matter over the last 400 million years of Phanerozoic time. ●, Predicted values. Sources of material: △, modern plants; ○, fossil leaves; □, fusain; +, coals; ◇, bulk organic matter from palaeosols. (Redrawn after Beerling and Woodward 1997.)

Carbon isotope signature of climatic forcing of plant growth recorded in fossils

Variations in the p_i/p_a ratio of leaves of C_3 plants are also reflected in $\delta^{13}C_p$ (equation 3), and are driven by changes in climatic conditions affecting the balance between photosynthetic and stomatal activity. Therefore where $\delta^{13}C_a$ is known (e.g. from direct measurements of CO_2 gas extracted from ice cores) or can be inferred from carbonates on geological time scales, variations in $\delta^{13}C_p$ may reflect climatic forcing of plant growth (Beerling 1997) and provide a palaeoclimatic signal. To interpret a climatic signal from Quaternary material it is important to obtain $\delta^{13}C_p$ variations from a single species and a specific plant organ down through the sequence because $\delta^{13}C_p$ can vary between species and between organs.

References

Beerling, D.J. (1997) Interpreting environmental and biological signals from the stable carbon isotope composition of fossilised organic and inorganic carbon. *Journal of the Geological Society* **154**, 303–309.

Beerling, D.J. and Woodward, F.I. (1997) Changes in land plant function over the Phanerozoic: reconstructions based on the fossil record. *Botanical Journal of the Linnaean Society* **124**, 137–154.

Farquhar, G.D. and Lloyd, J. (1993) Carbon and oxygen isotope effects in the exchange of carbon dioxide between terrestrial plants and the atmosphere. In: J.R. Ehleringer, A.E. Hall and G.D. Farquhar, eds. *Stable isotopes and plant carbon–water relations*, pp. 47–70. Academic Press, San Diego.

Jones, H.G. (1992) *Plants and microclimate: a quantitative approach to environmental plant physiology*. Cambridge University Press, Cambridge.

Vogel, J.C. (1993) Variability in carbon isotope fractionation during photosynthesis. In: J.R. Ehleringer, A.E. Hall and G.D. Farquhar, eds. *Stable isotopes and plant carbon–water relations*, pp. 29–46. Academic Press, San Diego.

4.3.4 Bathymetric Indicators

P.J. ORR

Introduction

Absolute water depth has relatively little effect on the bathymetric distribution of marine organisms except through its influence on hydrostatic pressure and the solubility of carbonate. Increase in hydrostatic pressure with depth is a limiting factor for organisms with in-ternal, gas-filled chambers, e.g. some fish, whales, and cephalopods. Oceanic water masses become undersaturated with respect to $CaCO_3$ with increasing depth. The depth at which significant dissolution of $CaCO_3$ begins is the lysocline. All carbonate is dissolved below the Carbonate Compensation Depth, typically at water depths between 3 and 4 km; this depth varies considerably with carbonate production and is shallower for aragonite. As in modern marine environments, the bathymetric distribution of most fossil organisms must have been controlled by factors such as wave or current energy, temperature, chemistry (including salinity and quantity of dissolved gases such as oxygen), light penetration, nutrient supply, competition for ecospace and resources, sedimentation rate, and substrate character (including the grain size and geotechnical properties of soft sediments). Reconstructions of palaeobathymetry using fossils are possible because changes in these factors tend to correlate with changes in water depth. The palaeobathymetric distribution of most fossils is therefore depth-related rather than depth-controlled.

The majority of palaeontological studies have attempted to ascertain the relative palaeobathymetry of fossil assemblages; fewer attempts have been made to determine absolute water depths. Both body fossils (microfossils and macrofossils) and trace fossils (ichnofossils) have been used.

Body fossils

Extrapolation of the bathymetric distribution of Recent taxa to fossil representatives (an application of taxonomic uniformitarianism) can be employed (see Dodd and Stanton 1990).

Light is a limiting factor for photosynthetic organisms; most Recent algae are restricted to the photic zone, although some can live at greater depths. Modern hermatypic, reef-building, scleractinian corals live in a symbiotic relationship with light-dependent zooxanthellae and are therefore restricted to the photic zone. This relationship appears to have persisted since the Mesozoic. The confidence with which a similar relationship can be inferred in other, older, reef-building organisms, such as Palaeozoic corals and stromatoporoids, is debatable (see discussion by Brett *et al.* 1993). The base of the photic zone does not translate easily to an absolute water depth; in modern marine environments its position varies, principally with latitude and water turbidity. In addition, the availability of light may not be the only limiting factor. The growth of modern reefs is strongly dependent on temperature; the maximum depth for reefs decreases away from tropical latitudes.

Planktic organisms are rarely used as depth indicators. Their postmortem transport is dominantly vertically downwards through the water column; they are therefore typically distributed across a range of water depths. Exceptions include the recognition of depth-related graptolite species in strata of Silurian age in the Welsh Basin: graptolites from all levels of the water column occur in deeper-water environments but only surface-living forms occur in shallower-water environments. The relative proportion of planktic to benthic foraminifera has been used by palaeontologists to assess relative water depths: planktic foraminifera are much less common in shallow, nearshore water than deep, open ocean water. As planktic foraminifera can live at depths of several hundred metres in open water, this is probably related to the lesser volume available for occupancy in shallow environments (see Dodd and Stanton

1990). A dominance of agglutinated foraminifera is often an indicator of depths close to, or in excess of, the Carbonate Compensation Depth, but it can also reflect low oxygen levels.

Most palaeobathymetric reconstructions are based on the biomineralized tissues of shelfal invertebrate benthos. Pioneering studies in the late 1960s identified five main, depth-related, benthic animal communities within clastic, level-bottom, shelfal strata of Llandovery age in the Welsh Borderland (Ziegler *et al.* 1968) (Fig. 4.3.4.1). Each was characterized by a particular brachiopod-dominated faunal assemblage, and named after a prominent brachiopod genus in that assemblage. In the early Upper Llandovery the nearshore *Lingula* community was succeeded offshore successively by the *Eocoelia*, *Pentamerus*, *Stricklandia*, and *Clorinda* communities (Fig. 4.3.4.1c). An understanding of the evolution of the relevant brachiopod lineages, and the recognition of taxonomically different communities as equivalents in terms of relative water depth, allowed the model to be extended to older and younger Llandovery strata of the region (Fig. 4.3.4.1b,d, respectively). This provided faunal evidence for a major transgression eastwards and southwards across the region during the Llandovery (Fig. 4.3.4.1e). The original communities have been reinterpreted in terms of Benthic Assemblages and the approach has been successfully used for other brachiopod-dominated faunas (see Pickerill and Brenchley 1991; Brett *et al.* 1993). Attempts to translate the relative palaeobathymetry of these Benthic Assemblages into absolute water depths have been more contentious; some degree of consensus has emerged via their integration with sedimentological and taphonomic criteria for recognizing water depth (Brett *et al.* 1993). Lower Palaeozoic trilobite communities have also proved useful in assessing relative palaeobathymetry. Modern palaeoecological studies favour rigorous, quantitatively based sampling methods; the significance of the datasets generated can then be tested statistically.

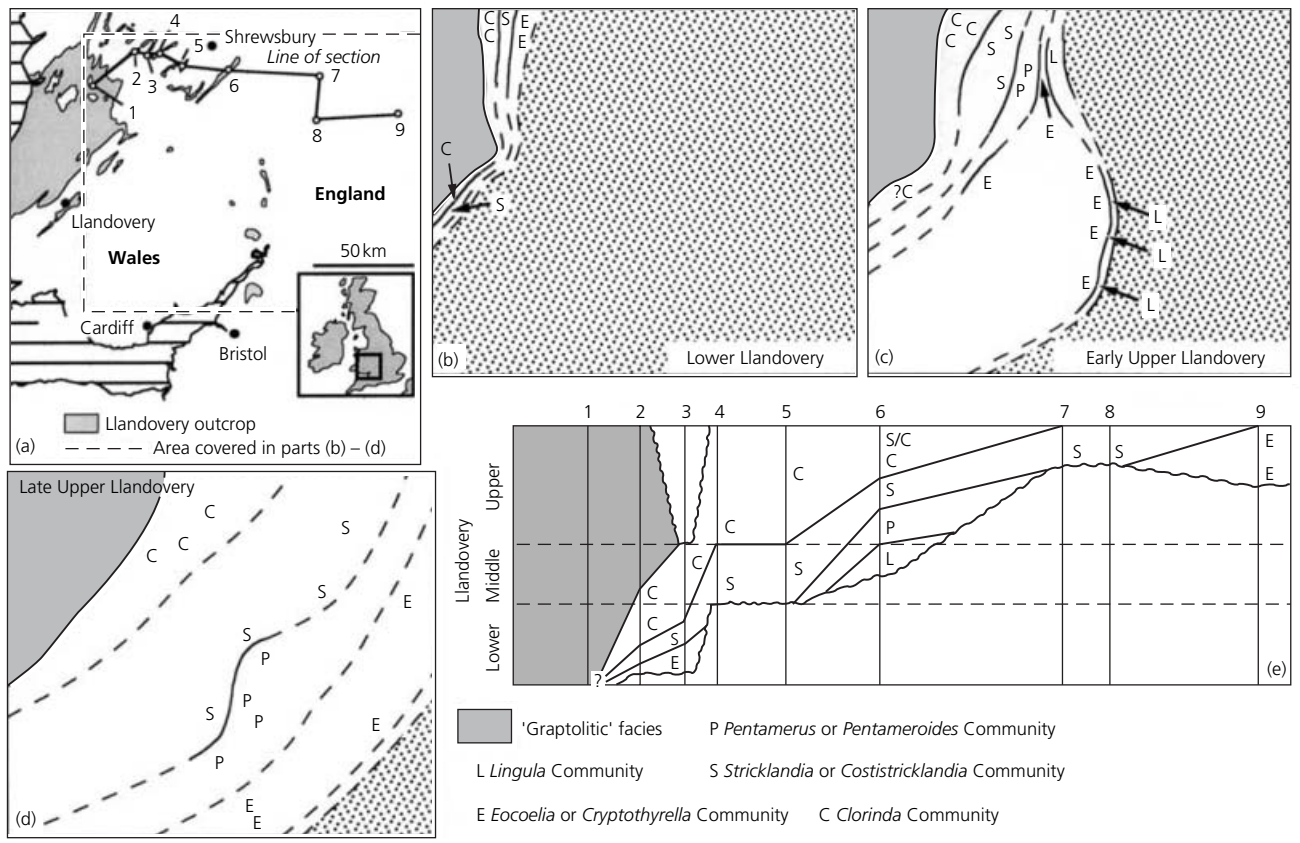

Fig. 4.3.4.1 Lower Silurian depth-related communities in Wales and the Welsh Borderland. (a) Location map showing study area and outcrop of Llandovery rocks. (b–d) Spatial distribution of the communities during the times indicated. (e) Plot of the distribution of the communities against time at each locality along the line of section indicated in (a). The succession of communities at a locality, and the progressive displacement of the communities eastwards with time, are the result of a major transgression eastwards and southwards during the Llandovery. (After Ziegler *et al.* 1968.)

Trace fossils

Recurrent combinations of sedimentary facies and trace fossils (ichnotaxa) within marine softgrounds have been interpreted as bathymetric indicators (see Bromley 1996); with increasing water depth these are the *Skolithos*, *Cruziana*, *Zoophycos*, and *Nereites* ichnofacies (*sensu* Seilacher 1967). Ichnotaxa reflect the behaviour of organisms on or within the substrate; the same ichnotaxon can be produced in very different environments, not necessarily by the same producer. The presence or absence of an individual ichnotaxon, even one characterizing an ichnofacies, cannot therefore be regarded as strong evidence for a particular water depth.

Clearly environmental conditions can be far from uniform at any given water depth. Idealized three-dimensional reconstructions such as Fig. 4.3.4.2 emphasize the heterogeneity of the marine environment and the implications of this for the distribution of ichnofacies (see additional examples in Bromley and Asgaard 1991). Trace fossils are sensitive environmental indicators; temporal changes in environmental conditions can result in a vertical succession of ichnofacies that mimic, but are not the product of, significant changes in water depth (Fig. 4.3.4.3).

Ichnofacies are a combination of biofacies and taphofacies (Bromley and Asgaard 1991). Infaunal communities are partitioned, or tiered, below the sediment–water interface into different ecological niches; this tiering is often accompanied by changes in the ecology of the organisms and, as a result, the trace fossils they produce. Erosion selectively removes the upper parts of the sediment column; the trace fossil record is therefore biased towards the activities of organisms at deeper levels. Where sedimentation exceeds erosion, however, the preservation potential of trace fossils produced within the upper tiers of the infaunal community is increased. Temporal changes in rates of sedimentation and erosion can therefore result in a succession of different ichnofaunal assemblages which have been produced in different tiers of the same endobenthic community. The variation is consequently taphonomic in origin and does not reflect changes in environmental conditions such as water depth. Temporal changes in water depth may induce changes in the composition of infaunal communities that are reflected in the trace fossils they produce. If accretion of sediment is limited, successive infaunal communities will rework the same sediment. In such cases, and depending on the intensity of bioturbation, only the last ichnofaunal assemblage to be emplaced may be preserved. The trace fossil evidence may therefore suggest that changes in water depth occurred more rapidly than was in fact the case.

The use of ichnofacies as a proxy for water depth can result in erroneous interpretations involving depths fluctuating hundreds of metres but separated strati-

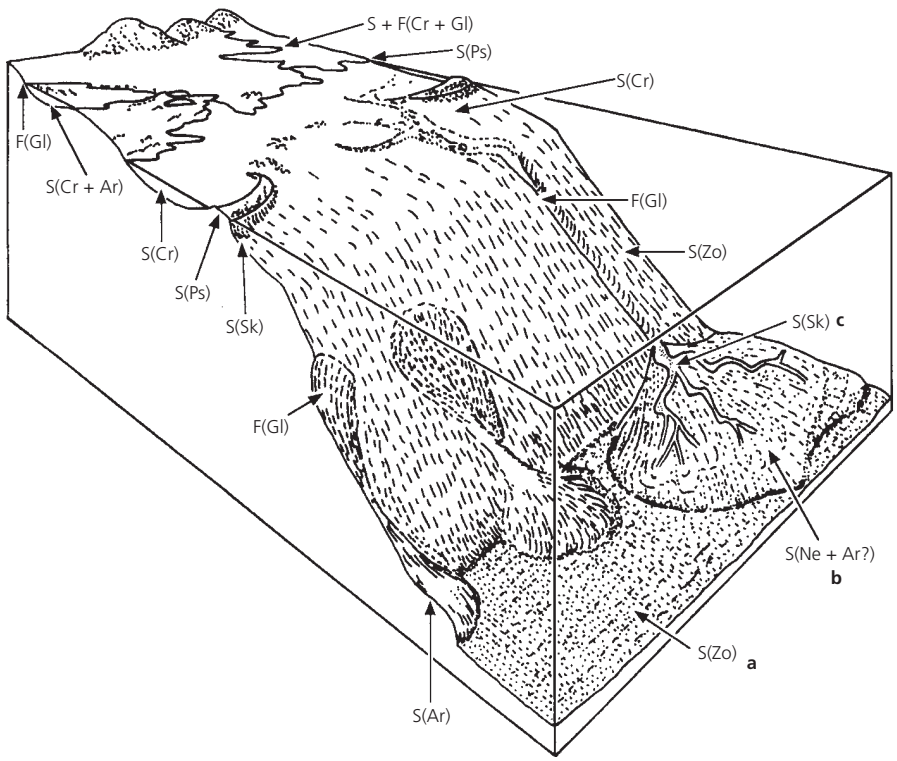

Fig. 4.3.4.2 Distribution of ichnofacies along a passive continental margin. The first letter indicates substrate consistency (F, firmground; S, softground), followed in parentheses by the ichnofacies (Gl, *Glossifungites*; Cr, *Cruziana*; Ar, *Arenicolites*; Ps, *Psilonichnus*; Sk, *Skolithos*; Zo, *Zoophycos*; Ne, *Nereites*). Letters **a**, **b**, and **c** correspond to the subdivisions of the idealized section in Fig. 4.3.4.3. (After Bromley and Asgaard 1991.)

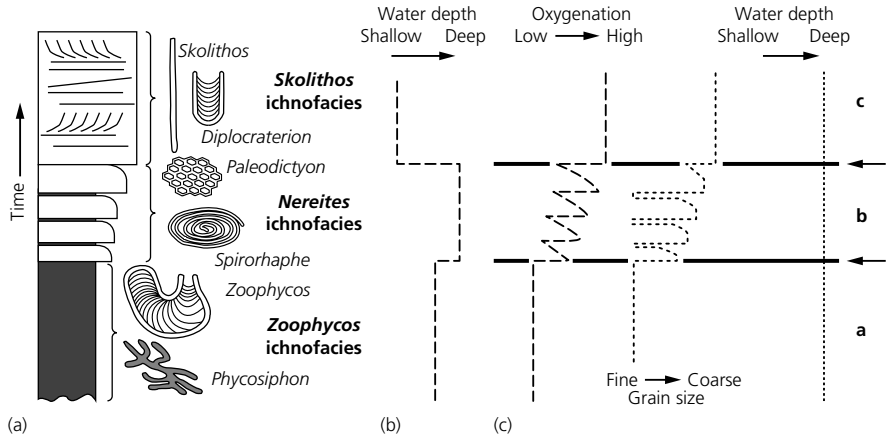

Fig. 4.3.4.3 (a) Idealized coarsening-upwards sequence with ichnogenera and corresponding ichnofacies identified. (b) Curve for relative water depth, based on the traditional interpretation of this succession of ichnofacies as reflecting palaeobathymetry. (c) The same succession of ichnofacies can be derived from environmental changes such as increases in oxygenation and grain size. These occur as a result of the lateral migration (lower arrow), and subsequently progradation (upper arrow), of a turbidite lobe; significant changes in water depth do not occur. Letters **a**, **b**, and **c** indicate the depositional environments shown in Fig. 4.3.4.2. (From Frey, R. and Pemberton, S.G. (1984) Trace fossil facies models. In: R.G. Walker, ed. *Facies models*, 2nd edn, pp. 189–207. Geoscience Canada Reprint Series; with permission of the Geological Association of Canada.)

graphically by very short distances. Generalized models of the palaeobathymetric distribution of trace fossils must be applied with caution; the vertical distribution of both ichnofaunal assemblages and ichnofacies can be explained by environmental changes other than water depth.

Conclusions

When using fossils in the interpretation of palaeobathymetry, assumptions based upon taxonomic uniformitarianism must be used with caution. The water depths inhabited by many organisms varied over geological time, and the taxonomic uniformitarian approach tends to decrease in precision with increasing geological age. The majority of fossil assemblages are time-averaged, i.e. the product of the mixing of a succession of communities. In such cases, the fossil assemblage may represent a composite sample of successive variations of the same community, or a mixture of two or more communities. It is essential to establish that the assemblages used for palaeobathymetric interpretations are autochthonous or parautochthonous; the extent of any postmortem redistribution must be assessed. Trace fossils, on the other hand, are usually autochthonous; having been emplaced within unconsolidated sediment, they do not survive re-working. The most reliable reconstructions of palaeobathymetry are based on an integrated approach; the comparison of independent palaeontological, taphonomic, and sedimentological criteria is encouraged.

References

Brett, C.E., Boucot, A.J. and Jones, B. (1993) Absolute depths of Silurian benthic assemblages. *Lethaia* **26**, 25–40.

Bromley, R.G. (1996) *Trace fossils: biology, taphonomy and applications*, 2nd edn. Chapman and Hall, London.

Bromley, R.G. and Asgaard, U. (1991) Ichnofacies: a mixture of taphofacies and biofacies. *Lethaia* **24**, 153–163.

Dodd, J.R. and Stanton, R.J. Jr (1990) *Paleoecology: concepts and applications*, 2nd edn. Wiley, New York.

Pickerill, R.K. and Brenchley, P.J. (1991) Benthic macrofossils as palaeoenvironmental indicators in marine siliciclastic facies. *Geoscience Canada* **18**, 119–138.

Seilacher, A. (1967) Bathymetry of trace fossils. *Marine Geology* **5**, 413–428.

Ziegler, A.M., Cocks, L.R.M. and McKerrow, W.S. (1968) The Llandovery transgression of the Welsh Borderland. *Palaeontology* **11**, 736–782.

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4.3.5 Atmospheric Carbon Dioxide—Stomata

J.C. McELWAIN

Introduction

The number of stomatal pores on the surface of fossil leaves is indicative of the CO_2 concentration of the ancient atmosphere in which they developed. This palaeobotanical proxy method, or 'palaeo-CO_2 barometer', is based on a well-documented inverse relationship between leaf *stomatal density* (the number of stomatal pores per mm^2) and atmospheric CO_2 (first demonstrated by Woodward 1987). A number of extant tree species have reduced their stomatal density by 40% in response to the anthropogenic rise in CO_2 over the last 200 years (Woodward 1987). This stomatal density response has been confirmed repeatedly in similar herbarium studies, controlled environment experiments, and across long time scales, where stomatal density has been shown to track the Quaternary glacial–interglacial cycle of CO_2 change, derived from analysis of air trapped in ice cores. The application of this technique to pre-Quaternary fossil plants has enabled the quantification of fluctuations in atmospheric CO_2 through the Phanerozoic, and has thus provided an independent means of validating models of CO_2 change (Berner 1998). Furthermore, the fossil stomatal method complements other independent proxy methods, derived from the stable carbon isotope composition of palaeosols and marine carbonates, respectively.

Rationale

The size and number of stomatal pores regulates the balance of CO_2 uptake by photosynthesis against the loss of water by transpiration. Plants are assumed to maintain their gas exchange at optimum levels, whereby photosynthetic gain is maximized against water loss. During periods of elevated CO_2 plants achieve the same carbon gain with fewer stomatal pores (i.e. lower stomatal density) and benefit by losing less water. Conversely, during periods of reduced CO_2 higher stomatal densities are required to achieve the same carbon gain, resulting in greater water loss via transpiration and lower water-use efficiency. As the stomatal pore acts at the interface between the atmosphere and plant, and stomatal density plays such an important role in gas exchange, fossil plant stomatal characteristics can provide a sensitive indicator of CO_2 fluctuations. Changes in stomatal characteristics can be observed directly by investigation of the cuticle (the waxy protective covering of the leaf surface). As cuticles are highly resistant to oxidation, fossil cuticles can be extracted easily from rock matrices by means of oxidizing agents.

Important considerations

Many environmental factors, including water stress, temperature, and humidity, influence leaf stomatal density indirectly by altering the size and/or spacing of the epidermal cells (the main tissue component of the leaf surface). However, atmospheric CO_2 and to a lesser extent light intensity are the only factors that influence the development of stomata from epidermal cell initials, thus directly affecting the number of stomatal pores on the leaf surface. Calculation of the *stomatal index*—a ratio of the number of stomatal cells to the total number of cells (epidermal and stomatal) on the leaf surface—therefore separates the direct effects of atmospheric CO_2 from the indirect effects of all other environmental parameters on stomatal numbers. However, before an unambiguous CO_2 signal can be obtained from fossil leaf stomatal characteristics, the inherent variation driven by light intensity needs to be removed by either of the following two strategies:

1 Collection of large sample sizes from different localities, so as to incorporate as much of the inherent variation in a species' stomatal characteristics as possible. Where shifts in both stomatal density and index are observed which significantly exceed the range of variation within samples, this may reasonably be attributed to the ubiquitous effects of CO_2.

2 Establish whether the leaves being investigated are 'sun' or 'shade' morphotypes, which can be assessed from morphological and anatomical characteristics of well-preserved examples.

Palaeo-CO_2 reconstructions from fossil stomata

Quantitative palaeo-CO_2 estimates for the Cenozoic have been made from fossil stomatal characteristics, using calibrations of stomatal density and index responses of *nearest living relative* (NLR) species to known concentrations of atmospheric CO_2. This methodology cannot be applied to Mesozoic and Palaeozoic CO_2 reconstruction, as extant species of vascular plants are not known earlier than the Late Tertiary. The stomatal parameters of these extinct pre-Tertiary fossil plants are therefore compared with *nearest living equivalent* (NLE) species, defined as species from the present day which are, as far as possible, of comparable ecological setting and/or structural similarity to their fossil counterparts. Semiquantitative estimates of pre-

Tertiary CO_2 are calculated from the *stomatal ratio*, defined as the ratio of the stomatal index of the nearest living ecological equivalent to that of the fossil taxon (McElwain 1998). Stomatal ratios are standardized against Berner's (1998) long-term carbon cycle model CO_2 estimates for the Phanerozoic by means of either one of two standards (Fig. 4.3.5.1):

1 A Recent standard, assuming a value of 1 for the stomatal ratio today, equivalent to 360 ppm CO_2.

2 A Carboniferous standard where a stomatal ratio of 1 is equivalent to 600 ppm CO_2. This was achieved by standardizing the stomatal ratios of a number of fossil conifers from the Upper Carboniferous (stomatal ratios of 0.58) against Berner's (1998) model estimates. The Carboniferous was chosen rather than other intervals in the Phanerozoic because, according to other palaeo-CO_2 proxies and modelling estimates, the Carboniferous CO_2 was very similar to the present ambient concentration (360 ppm).

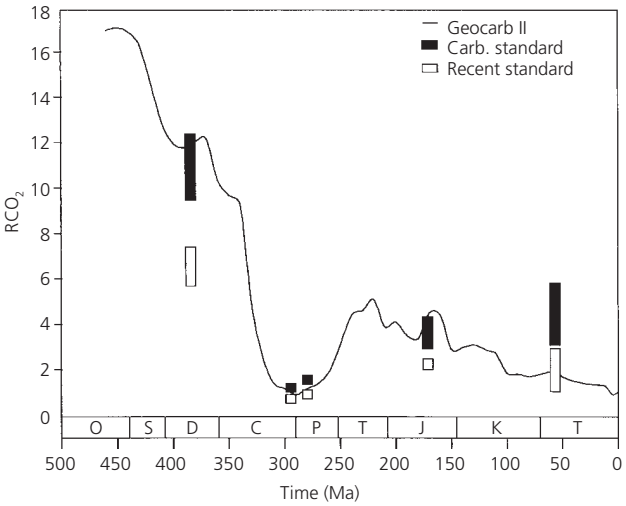

Fig. 4.3.5.1 Estimates of palaeo-atmospheric CO_2 for the Phanerozoic calculated from the stomatal ratios of fossil plants based on a Carboniferous standard (black solid bars) or a Recent standard (white bars), as described in the text, compared with estimates of Berner's (1998) Geocarb II model. RCO_2 represents a ratio of the atmospheric CO_2 concentration at some time in the past to that of the preindustrial concentration of 300 ppm. Palaeo-CO_2 estimates for the Lower Devonian were based on stomatal ratios (in parentheses after each species) of *Aglaophyton major* (6.2) and *Sawdonia ornata* (4.8); for the Upper Carboniferous on *Swillingtonia denticulata* (0.58); for the Lower Permian on *Lebachia frondosa* (0.79); for the Middle Jurassic on *Brachyphyllum mamillare* (1.65), *B. crucis* (2.08), *Pagiophyllum kurrii* (2.11), *P. ordinatum* (1.83), and *P. macullosum* (2.09); and for the Middle Eocene on *Litsea hirsuta* (1.61), *L. bournensis* (1.68), *L. edwardsii* (1.65), *Lindera cinnamomifolia* (2.54), and *Lindera* sp. A (1.65).

Record of Phanerozoic CO_2

Quantitative CO_2 reconstructions have been obtained from Miocene, Pliocene, and Early Pleistocene fossil oak leaves which suggest that the palaeo-CO_2 fluctuated between 280 and 370 ppm, based on the calibration of modern oak stomatal density and index to known concentrations of CO_2. Beyond the Miocene, fossil plant stomatal densities vary inversely with model estimates of palaeo-CO_2 (Beerling and Woodward 1997). The stomatal ratio approach applied to Middle Eocene, Middle Jurassic, Upper Permian, Lower Carboniferous, and Lower Devonian fossil plant species yields results (Fig. 4.3.5.1) in good agreement with both modelling and estimates from palaeosol and marine carbonate based proxies (see Berner 1998).

References

Beerling, D.J. and Woodward, F.I. (1997) Changes in land plant function over the Phanerozoic: reconstructions based on the fossil record. *Botanical Journal of the Linnaean Society* **124**, 137–153.

Berner, R.A. (1998) The rise of plants and their effects on weathering and atmospheric CO_2. *Science* **276**, 544–546.

McElwain, J.C. (1998) Do fossil plants signal palaeoatmospheric CO_2 concentration in the geological past? *Philosophical Transactions of the Royal Society of London B* **353**, 83–96.

Woodward, F.I. (1987) Stomatal numbers are sensitive to increases in CO_2 from pre-industrial levels. *Nature* **327**, 617–618.

4.3.6 Climate—Wood and Leaves

D.R. GREENWOOD

Introduction

The plant macrofossil record is dominated by leaves and woody axes. Because assemblages of these organs are commonly autochthonous to parautochthonous, macrofossils are a record of local plant communities and therefore of local climate (Greenwood and Wing 1995). Temperature and water availability influence both transpiration and leaf metabolic processes and thus leaf morphology, and the constancy and length of favourable growth conditions each year are reflected in wood anatomy. Extant woody vegetation, particularly angiosperm-dominated vegetation, therefore shows trends of physiognomy along temperature and rainfall

gradients. Some attributes appear to be threshold responses (i.e. they reflect the impact of limiting factors as stressors), where the attribute is present in response to the stressor, but is absent where the stressor is absent.

Correlations between key attributes of vegetational physiognomy and climate have been used to reconstruct Late Cretaceous and Cenozoic palaeoclimates. Most approaches are based on the proportions of species in a local flora (modern analogue or fossil assemblage) possessing particular characters, and so rely on at least a parataxonomic sorting (i.e. individuation of the assemblage into discrete parataxa, without necessarily identifying their taxonomic relationships) of assemblages (Woodcock and Ignas 1994; Wolfe 1995). Floras respond to local climate conditions and this imposes limitations on regional reconstruction of palaeoclimate, necessitating consideration of facies effects and time-averaging (i.e. collection of successive strata within an excavation site and between sites as a single 'flora'). Approaches based on specimen counts as opposed to taxonomic diversity may afford greater fidelity as a result of removal of taxonomic blurring between different workers and quantification of taphonomic biases, but such approaches remain largely undeveloped (Greenwood and Wing 1995).

Wood anatomy

Several factors act to confound the use of wood as a palaeoclimatic proxy. Some aspects of wood anatomy may represent threshold responses to a limiting factor, such as water stress or freezing. Other anatomical attributes may be absent from some lineages, or restricted to the most advanced members of evolutionary series (e.g. vessel elements). Two main aspects of wood structure appear sensitive to climate, although more research is required to redress deficiencies in the quantitative understanding of covarying anatomical–climate responses (Woodcock and Ignas 1994).

Cellular architecture

Precipitation and temperature may be reflected in the presence, character, abundance, and distribution of parenchyma, vessels, or other specialized cells, some of which are prone to air embolism or freezing damage. For example, ring porosity (i.e. wood with large-diameter vessels) is correlated with precipitation, but ring-porous wood is absent from climates where temperature minima are less than –40°C because trees in these climates utilize supercooling to prevent freezing damage.

Tissue organization

Annual growth rings indicate seasonality of temperature or precipitation. Annual variation of ring widths (or the size of xylem cells within rings, i.e. wood density) is correlated with precipitation. The degree of transition to late wood displayed at the termination of seasonal growth is correlated with the rapidity and severity of the transition to unfavourable conditions. The prevalence of homocellular rays (i.e. composed solely of one cell type) and storied rays (i.e. arranged in horizontal tiers in tangential section) varies with temperature.

Leaf physiognomy

Theoretical and experimental studies have demonstrated that leaf attributes ('leaf or foliar physiognomy'), such as size, shape, and the prevalence of features such as drip tips, vary along environmental gradients. This variation reflects an adaptive compromise between the need to capture light energy and manage heat gain and loss, and, at the same time, maximize the efficiency of gas exchange, transpiration, and photosynthesis. Quantitative analyses of modern vegetation leaf physiognomy and climate responses along environmental gradients have been largely univariate, but multivariate approaches integrate multiple leaf characters and climatic parameters. They have been used to estimate temperature and precipitation (to varying degrees of fidelity) for the Late Cretaceous and Cenozoic using woody dicot leaf physiognomy.

Temperature

Leaf margin analysis (LMA) was based on the (univariate) observation that the proportion of woody dicot species with 'non-entire' (toothed or lobed) leaf margins varies proportionately along a mean annual temperature (MAT) gradient (Wolfe 1995). This was quantified for East Asian mesic forests (Fig. 4.3.6.1a), and appears robust in speciose (i.e.>20 species) predominantly deciduous broadleaved regional floras (e.g. North America, Europe, and Asia). It is less robust in predominantly evergreen broadleaved regional floras. In Australian mesic forests tree leaf size is correlated with MAT, but a quantitatively different relationship is present for predominantly deciduous tropical and temperate broadleaved vegetation (Fig. 4.3.6.1b) with leaf size departing significantly from the regression line for sites from these vegetation types. Multivariate approaches have been based largely on the CLAMP (climate leaf analysis multivariate program) dataset of primarily Western Hemisphere vegetation (Wolfe 1995). Canonical correlation analysis (CCA) (Fig. 4.3.6.1c) and multiple regression (MR) analyses of this dataset combined several leaf characters, but leaf margin type represented a significant component of the relationship between physiognomic states and temperature. CLAMP (either approach)

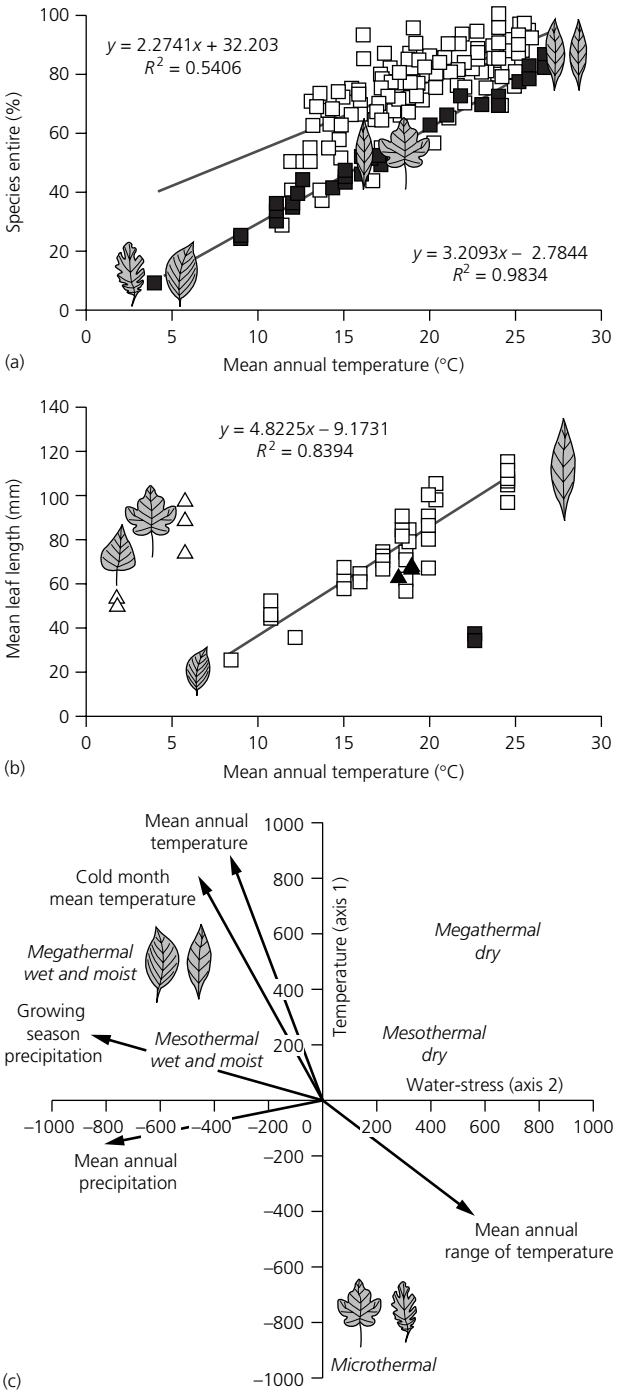

Fig. 4.3.6.1 Plots of correlations of leaf features and major climate parameters. Regression equations and statistics presented on bivariate charts. Leaf cartoons on charts indicate the main leaf character states varying with the climate parameters indicated. (a) The proportion of species in extant local floras with entire leaf margins vs. mean annual temperature; ■, East Asian mesic forests; □, eastern Australian mesic and dry-season deciduous forests; sources cited by Wolfe (1995), Greenwood and Wing (1995), and unpublished; n = 206, all sites > 20 spp. (b) The mean length of all specimens of leaves in extant forest floor litter samples vs. mean annual temperature; □, eastern Australian mesic forests; ■, Australian dry-season deciduous forests; ▲, south-eastern USA semideciduous forests; △ Canadian deciduous forests; sources cited by Greenwood and Wing (1995) and unpublished. (c) Canonical correspondence analysis plot of vectors of climate parameters of samples of the CLAMP database; axis 1 has an eigenvalue of 0.118 and accounts for 45.9% of variance of leaf physiognomy, and 64.5% of the variance of the physiognomy and environment relationship; the length of the vectors indicates the relative importance of the parameters. (c, Adapted from Wolfe 1995; with permission from the *Annual Review of Earth and Planetary Sciences*, vol. 23 © 1995 by Annual Reviews.)

allows MAT to be estimated with small standard errors (e.g. CCA ± 0.7–1.0°C; MR ± 2.0°C). Its application, however, is currently limited by the geographically restricted coverage of the modern analogue dataset and effective sampling distortions for species-poor ancient floras.

Physiognomic approaches to reconstructing temperature seasonality were based on matching fossil floras to climate-controlled regional vegetation formations, or biomes. The potential temperature range was determined from a climate nomograph that plotted these biomes in a two-axis climate space (Wolfe 1995). The CLAMP modern analogue dataset has permitted direct quantitative estimates of winter temperatures (e.g. CCA ± 1.5–2.0°C; MR ± 3.6°C), but is problematic as MAT and winter temperatures are autocorrelated. For example, estimates of winter temperatures for Eocene floras from CLAMP (MR) are colder than from nearest living relative analogy, a discrepancy that may highlight a systematic error for winter temperature estimates from CLAMP (Greenwood and Wing 1995). Some leaf physiognomic temperature responses may be threshold responses to the incidence of freezing (or other stressors), which is reflected in the different patterns seen in broadleaved evergreen vs. deciduous forests (Fig. 4.3.6.1a,b). Seasonal temperature ranges are greater in the Northern than in the Southern Hemisphere today (for the same MAT), and were likely also under warmer and more equable climates in past geological periods. Thus the emphasis on Northern Hemisphere sites in the CLAMP dataset emphasizes the systemic errors introduced by the autocorrelation of MAT and winter temperatures. Broadening the modern analogue dataset will address this problem, by including sites with quantitatively different relationships between these climate parameters. Temperature estimates will also be in error where deciduousness is a response to high-latitude winter darkness, and not winter freezing (e.g. Eocene and other warm phases of the Cenozoic).

Precipitation

Leaf form is unlikely from theoretical considerations to

respond directly to annual precipitation, particularly where there is a significant period when plants are dormant, and so threshold responses may be dominant. Leaf form is more likely to be a proxy for growing season water availability, reflecting some combination of temperature (potential for evaporation), evaporation (actual water loss from tissue), and rainfall (water supply). Using CLAMP and CCA, mean growing season precipitation (MGSP) can be estimated (± 120 mm), but leaf form appears insensitive where MGSP is >1450 mm (Wolfe 1995). Leaf size alone may act as a reliable measure of palaeoprecipitation (Wilf *et al*. 1998); univariate approaches, however, may obscure the combined influences of other factors.

References

Greenwood, D.R. and Wing, S.L. (1995) Eocene continental climates and latitudinal gradients. *Geology* **23**, 1040–1048.

Wilf, P., Wing, S.L., Greenwood, D.R. and Greenwood, C.L. (1998) Using leaves as paleoprecipitation indicators: an Eocene example. *Geology* **26**, 203–206.

Wolfe, J.A. (1995) Paleoclimatic estimates from Tertiary leaf assemblages. *Annual Review of Earth and Planetary Sciences* **23**, 119–142.

Woodcock, D.W. and Ignas, C.M. (1994) Prevalence of wood characters in Eastern North America: what characters are most promising for interpreting climates from fossil wood? *American Journal of Botany* **81**, 1243–1251.

4.3.7 Climate—Modelling using Fossil Plants

G.R. UPCHURCH Jr

Introduction

Fossil plants have long provided important evidence for major changes in vegetation and climate through geological time. The recognition that vegetation can also regulate climate, coupled with the development of new climate models, has prompted interest in how vegetational change influenced past climate. Vegetation impacts the energy balance of the land surface through its effects on albedo, surface roughness, and evapotranspiration, and impacts important geochemical processes (such as surface weathering) which determine the concentration of atmospheric CO_2.

Atmospheric General Circulation Models

A climate model simulates one or more processes within the climate system (see Henderson-Sellers and McGuffie 1987). An Atmospheric General Circulation Model (or AGCM) simulates the three-dimensional circulation of the atmosphere by solving the equations for conservation of mass, energy, and momentum. An AGCM divides the Earth's surface into a series of grids, and the atmosphere into a series of pressure levels, for computational efficiency. Land/ocean distribution, elevation, concentration of greenhouse gases, solar radiation, and characteristics of the ocean and land surface are set in the model at predetermined values (or boundary conditions). The model then calculates climate fields such as temperature, precipitation, and pressure, which are either displayed as maps (Fig. 4.3.7.1) or as average values plotted against latitude (Fig. 4.3.7.2).

Climate modellers perform sensitivity studies to understand the climate system. A sensitivity study consists of one control simulation and additional simulations where one or more boundary conditions are altered from the control values (e.g. atmospheric pCO_2). Such a study demonstrates the importance of different boundary conditions in the model climate and their effects on the climate system. The changes seen in the study are then compared with changes documented from climate data. For palaeoclimates, congruence between climatic changes seen in a sensitivity study and climatic changes seen in the geological record implies that the factors investigated in the sensitivity study were important in past climatic change.

Vegetation

Physical characteristics of vegetation are set as boundary conditions in the AGCM, which are then used to calculate fluxes of energy, water vapour, and momentum between the land surface and the atmosphere. Physical characteristics of vegetation include canopy height, fractional cover, Leaf Area Index (LAI), stomatal resistance (the leaf's resistance to diffusion of water vapour and CO_2), reflectance, and rooting depth. For modelling studies of Recent climate, these input values are derived from field measurements of vegetation (e.g. Dorman and Sellers 1989). For studies of palaeoclimate, input values are inferred from the closest modern analogue vegetation (Upchurch *et al*. 1998), measured directly from fossils, or calculated by a submodel that derives vegetation type from climate fields in the AGCM (e.g. Claussen *et al*. 1998).

Model vegetation is either fixed or allowed to change within a simulation. Fixed vegetation sets the physical characteristics of vegetation at predetermined values for the full length of the model simulation. Vegetation can respond to climate physiologically but cannot change in terms of height, LAI, or abundance of life forms (e.g. the abundance of deciduous trees vs. grasses). Coupled and interactive vegetation sets the vegetation at initial values

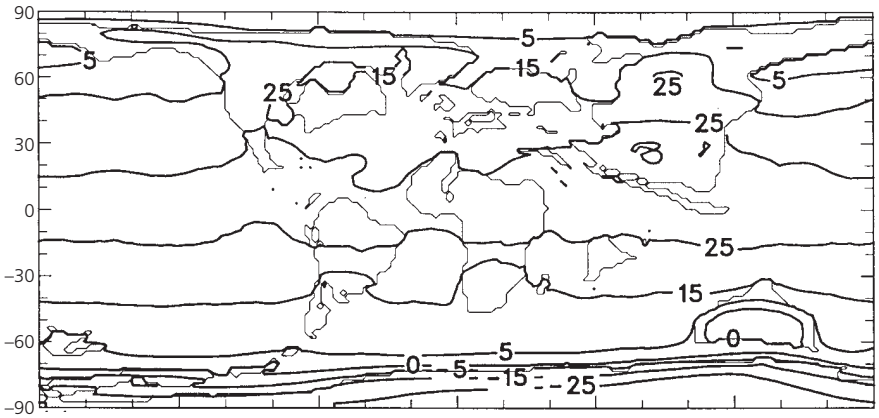

Fig. 4.3.7.1 Simulation of July surface temperature for the latest Cretaceous using the GENESIS Earth-systems model and a realistic distribution of palaeovegetation. (From Upchurch *et al.* 1998; with permission of the Royal Society of London.)

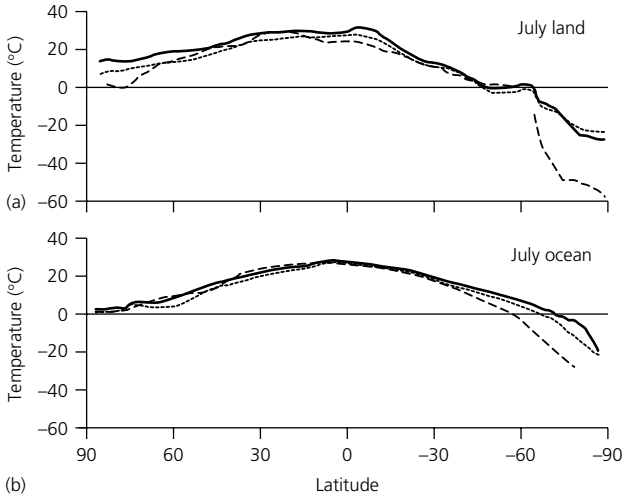

Fig. 4.3.7.2 Simulation of latest Cretaceous July surface temperature for land (a) and ocean (b) using the GENESIS Earth-systems model. Temperatures are zonally averaged (i.e. represent the average for a given line of latitude). The solid line represents the simulation that used realistic palaeovegetation, while the dotted line represents the simulation that used global bare soil. The dashed line represents the control simulation for the Recent. (From Upchurch *et al.* 1998; with permission of the Royal Society of London.)

to start the simulation, then allows the physical characteristics of the vegetation to change through the full length of the simulation in response to climate. Vegetation is determined by a submodel in the AGCM that takes temperature, precipitation, and other values for the land surface and calculates the vegetation that should occur there. Vegetation type therefore can change from the initial type as the simulation proceeds. Changes in model vegetation, in turn, can cause changes in model climate.

Each type of model vegetation allows the climate modeller to investigate a particular set of problems. Fixed model vegetation provides a straightforward means of determining the climatic impact of vegetational change or altered features within vegetation. Fixed vegetation, for example, can determine in which regions of the Earth's surface vegetational change can significantly alter climate. In addition, when combined with geological data, it can determine whether the model can simulate the climate necessary to sustain vegetation that existed in a given region in the past (Upchurch *et al.* 1998). Coupled and interactive vegetation also can address these questions but are best suited to understanding aspects of the climate system where initial conditions and threshold effects are important. For example, coupled and interactive vegetation can demonstrate the possibility of multiple equilibrium states of the vegetation–climate system under certain solar insolation regimes (Claussen *et al.* 1998).

Case studies

Three case studies illustrate how modelling climate with palaeovegetation can elucidate the role of vegetation in past climatic changes. For the Late Cretaceous, fixed model vegetation was used to demonstrate that palaeovegetation actively contributed to warm global climate (Upchurch *et al.* 1998). Simulation of climate with a realistic distribution of palaeovegetation causes global warming of 2.2°C and high-latitude warming of up to 12°C relative to simulation with global bare soil. The bare soil simulation produces high-latitude temperatures too cold to support the areally extensive polar forests documented for the Late Cretaceous. In contrast, the realistic vegetation simulation produces sufficient summer warmth to support polar forests, largely through decreases in surface albedo and masking of snow cover by trees. Cretaceous polar forests therefore helped to create the climatic conditions necessary for their persistence on the landscape.

For the Late Cenozoic, fixed model vegetation was used to demonstrate how the rise of grassland, desert, and tundra vegetation could have caused global cooling (Dutton and Barron 1997). Using Miocene palaeogeography, simulation of climate with the current latitudinal distribution of vegetation produces global cooling of 1.9°C relative to simulation with realistic Early Miocene vegetation, in which forests occupy most vegetated regions. Global cooling results from the increased surface albedo of grassland, desert, and tundra relative to forests and is most pronounced at high latitudes. This is because tundra vegetation of high latitudes is completely covered by snow during the winter, whereas forest vegetation has branches that project above the snow cover and absorb more solar radiation than snow. Vegetational change therefore amplified late Cenozoic cooling, which was caused by such factors as decreased atmospheric pCO_2, changes in palaeogeography, and increases in ice volume.

For the Pleistocene and Recent, coupled vegtation was used to demonstrate how interaction between solar insolation regime and the distribution of vegetation can produce multiple vegetation–climate equilibria (Claussen *et al*. 1998). For the insolation regimes of the Recent and last glacial maximum, simulation of climate with different initial distributions of vegetation shows that two equilibrium states exist for North African vegetation and climate: (1) a dry Sahara, which corresponds with the known distribution of Recent and past vegetation; and (2) a wetter Sahara, with a northward expansion of savannah and shrub land. However, for the insolation regime of the mid-Holocene (6000 BP) only one equilibrium state exists: a wet Sahara, which corresponds well with palaeoclimatic indicators.

Results from these and other climate modelling studies provide a rigorous and repeatable means of investigating vegetation–climate interactions in the geological past. Future studies will continue to demonstrate an important linkage between biotic change and global climate change in the geological past.

References

Claussen, M., Brovkin, V., Ganopolski, A., Kubatzki, C. and Petoukhov, V. (1998) Modelling global terrestrial vegetation–climate interaction. *Philosophical Transactions of the Royal Society of London B* **353**, 53–63.

Dorman, J.L. and Sellers, P.J. (1989) A global climatology of albedo, roughness length and stomatal resistance for atmospheric general circulation models as represented by the Simple Biosphere Model (SiB). *Journal of Applied Meteorology* **28**, 833–855.

Dutton, J.F. and Barron, E.J. (1997) Miocene to present vegetation changes: a possible piece of the Cenozoic cooling puzzle. *Geology* **25**, 39–41.

Henderson-Sellers, A. and McGuffie, K. (1987) *A climate modelling primer*. John Wiley, New York.

Upchurch, G.R. Jr, Otto-Bliesner, B.L. and Scotese, C. (1998) Vegetation–atmosphere interactions and their role in global warming during the latest Cretaceous. *Philosophical Transactions of the Royal Society of London B* **353**, 97–112.

4.3.8 Climate—Quaternary Vegetation

T. WEBB

Introduction

The large climate changes of the Quaternary, whether involving variations in monsoonal intensity or ice sheets, have left an unmistakable imprint on the spatiotemporal patterns of regional- to global-scale vegetation (Huntley and Webb 1988; Bartlein *et al*. 1998). Deciphering this climatic signal is a challenge to palaeoecologists and palaeoclimatologists because many biotic or other non-climatic factors also influence the vegetation. Like all potential climatic instruments, the vegetation record must be measured at the right temporal and spatial scales to yield clear, interpretable climatic evidence. For example, palaeoecological data from small forest-covered hollows may register a plant succession that masks climatically induced trends. Site selection, time-series analysis, and mapping techniques all help to identify and emphasize those aspects of the fossil record that are sensitive to climate.

Data selection and analysis

Because climate varies on all time and space scales, climatically sensitive records need further selection and tuning if they are to document a particular scale of climate change. Vegetation, like climate, is the sum of many signals, and decade-to-century scale variations require very different sampling strategies to those on a million-year scale. Ample independent records of climate from isotopes, moraines, plankton, and even climate models provide Quaternary palaeoecologists with a guide to the spatial and temporal variations to expect. For example, a 3-million-year sequence sampled every 15 000 years will not record precession-driven monsoonal variations with a period of 20 000 years, but it can show how a 100 000-year cycle became the dominant period of forcing during the last million years. On the

other hand, sampling intervals of 50 years or less are needed in sequences from the last 1000 years if the climate variations associated with the Little Ice Age (AD 1450–1850) are to be recorded. Regional differences among soils can influence the sensitivity of the vegetation to variations in temperature and moisture. Spatial averaging can remove intersite differences and emphasize the regional-to-continental vegetational gradients that are influenced by climate. Moving averages within time series can likewise remove short-term non-climatic variations among samples and yield long-term records highly tuned to climate.

Calibration of the record in climate terms

The northward movement of forest as an interglacial develops, or the oscillation between prairie and forest as moisture varies, indicate the worth of calibrating these vegetation changes in terms of temperature and precipitation (Bartlein *et al*. 1984). The parallel patterns of vegetation and climate gradients today provide the empirical basis for calibration, and four approaches have been followed to obtain quantitative estimates from fossil data:

1 'Palaeoecological' equations can be calculated in which climate variables are modelled as a function of pollen abundances, and different forms of multiple regression are used to calculate the parameters (Bartlein *et al*. 1984).

2 'Ecological' equations, in the form of response surfaces, express pollen abundance or presence/absence in terms of climate variables. The response surfaces are then used to estimate past temperatures (Bartlein *et al*. 1998).

3 Dissimilarity measures can be used to match fossil pollen samples with modern samples; if the match is close enough, the climate associated with the modern sample provides an estimate of that prevailing when the fossil sample was preserved. Lake-level evidence and indicator species are sometimes included in the analysis to help identify samples that are best matches (Guiot *et al*. 1993).

4 Taxa may be reclassified as plant functional types for which climatic limits are known, and the data interpreted in terms of these limits. This latest approach is useful for general interpretations of trends and gradients across a continent, but can be too coarse for interpreting data at individual sites.

Each empirical interpretative approach relies on the assumption that the present is the key to the past. How literally this assumption is applied depends on the method and the precision of the estimates. Few would dispute that present ecological relationships allow the inference that abundant oak pollen implies warmer conditions than abundant spruce pollen at any time in the Quaternary. However, estimates of a July mean temperature of $24 \pm 1°C$ based on 40% oak pollen and 2% spruce pollen are less reliable for any time except the mid- to late Holocene. Many new methods, including the output from climate models and the evidence of geochemical records, enable such estimates to be tested. Palaeoecologists need to recognize, however, that climate estimates are only a guide to answering the important questions of how and why the climate changed.

The assumption that a given scale and type of vegetational variation is in equilibrium with climate is central to the climatic interpretation of past vegetation. Because climate is always changing, however, only some form of dynamic equilibrium is possible, which is gauged by the ratio of the response time of the vegetation to the period of climate forcing. The scale of forcing varies from years for El Niño and the Southern Oscillation, to tens and hundreds of thousands of years for orbital variations, to even millions of years for tectonic variations. Recent calibration of climate variations during Younger Dryas time (13 000–11 000 BP) indicates response times of 500 years or less in the vegetation, and even shorter response times prevailed during the Little Ice Age. Such short response times make the vegetation sensitive to a wide spectrum of climate variations, from centuries to millions of years.

References

Bartlein, P.J., Webb, T. III and Fleri, E.C. (1984) Holocene climatic change in the northern Midwest: pollen-derived estimates. *Quaternary Research* **22**, 361–374.

Bartlein, P.J., Anderson, P.M., Anderson, K.H., Edwards, M.E., Thompson, R.S., Webb, R.S., Webb, T. III and Whitlock, C. (1998) Paleoclimate simulations for North America for the past 21,000 years: features of the simulated climate and comparisons with paleoenvironmental data. *Quaternary Science Reviews* **17**, 549–585.

Guiot, J., Harrison, S.P. and Prentice, I.C. (1993) Reconstruction of Holocene precipitation patterns in Europe using pollen and lake-level data. *Quaternary Research* **40**, 139–149.

Huntley, B. and Webb, T. III, eds. (1988) *Vegetation history: handbook of vegetation science*, Vol. 7. Kluwer Academic Publishers, Dordrecht, The Netherlands.

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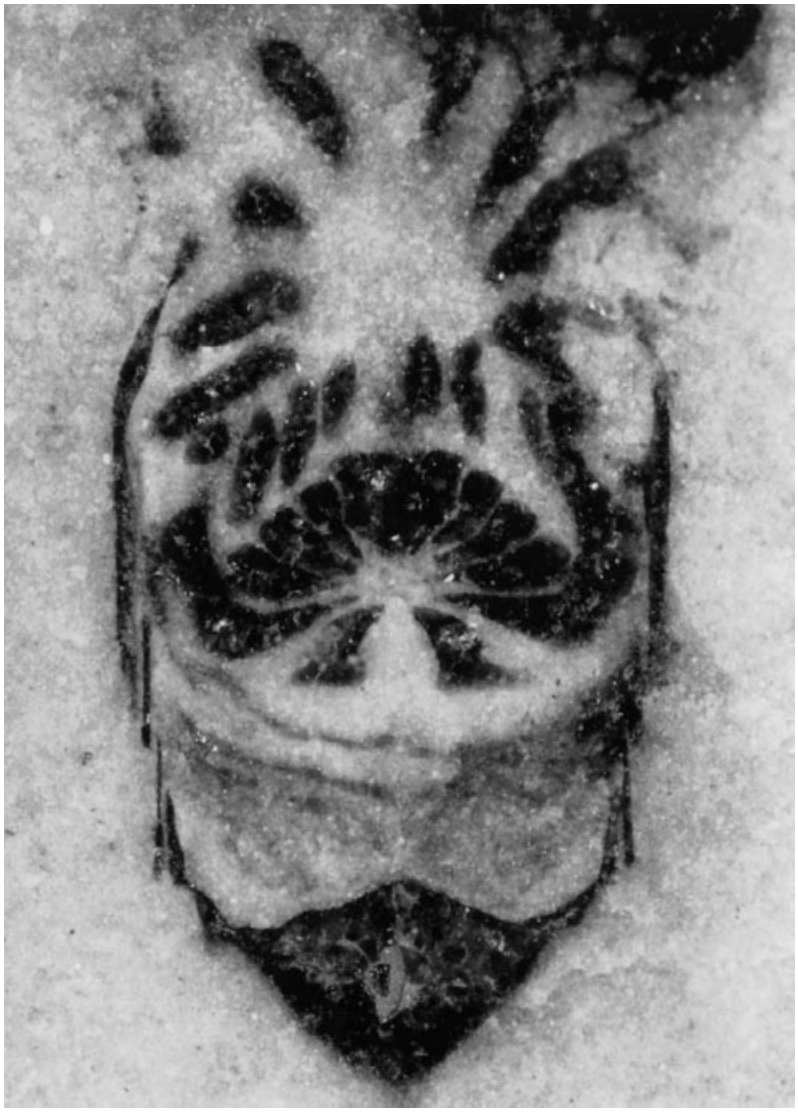
5
SYSTEMATICS, PHYLOGENY, AND STRATIGRAPHY



The arthropod *Offacolus kingi* revealed by splitting a concretion from the Silurian (Wenlock Series) of Herefordshire, England, ×36. (Photograph courtesy of M. Sutton, Oxford.)

5.1 Morphology and Taxonomy

5.1.1 Quantifying Morphology

R.E. CHAPMAN and D. RASSKIN-GUTMAN

Introduction

One of the great difficulties inherent in doing research in an historical science such as palaeontology is the paucity of available data. Almost all aspects of the palaeobiology of extinct taxa must be inferred indirectly from only a few lines of evidence. Significant data can be derived from the distribution and palaeoecology of organisms, but almost all other information must be derived from morphology.

The quantification of morphology aims at searching for meaningful patterns in collections of biological structures. As such, it reflects a basic tenet of science: that there are common, objective grounds upon which models of similarity and variation can be established in order to understand relationships among natural structures. When palaeontologists quantify morphology, they seek to reduce a specimen to a more simplified model, a numerical abstraction. This process, referred to as morphometrics, is necessary in order to isolate and stress the features that are being analysed. The abstraction is done by converting biological characters into mathematical descriptors and/or statistical variables.

Modelling morphology

The approach used to quantify morphology depends on the nature of the research and the objects being studied. In some cases, selected anatomical regions are analysed. In others, the overall shape of the whole organism is quantified, most commonly in studies of taxa with shapes that can be simply described, such as the accretionary growth of gastropods. In all cases, once the morphology to be analysed is determined, methods have to be developed to quantify it so that variation in both size and shape can be analysed objectively. Three steps are involved in this process: data acquisition, data analysis, and biological interpretation. Many options are available for extracting data from specimens, including standard tools (e.g. rulers, calipers) and more automated devices typically used in conjunction with computers (e.g. two- and three-dimensional digitizers, image analysis systems, laser and CT scanners). Measurements are then subjected to univariate, bivariate, and multivariate statistical analyses to look for possible trends within the data. Ultimately, a taphonomic or biological explanation is hypothesized for the observed patterns, e.g. preservational effects, ontogeny, heterochrony, sexual dimorphism, behaviour, evolution, variation, and/or functional considerations.

The importance of mathematical modelling in morphology, today known as theoretical morphology, was established by Thompson (1917) in his book *On Growth and Form*, which built on contemporary research and historical work going back to the Greek philosophers, as well as scientists/artists such as Leonardo da Vinci and Albrecht Dürer. Thompson set the foundations upon which the two major exploratory and analytical tools were established: the 'theory of transformation' and the study of 'morphospaces.'

The *theory of transformation*, originated by Thompson and developed subsequently, provides a way to 'relate' close forms by a mathematical function in order to model the processes involved in evolutionary or ontogenetic change. The theory, however, has evolved into the modern school of geometric morphometrics (Bookstein 1991) which mostly focuses on variation at intraspecific or interspecific levels. Here morphology is quantified as coordinate values, either for points along an outline or for landmark points found on each specimen. These coordinate values can be analysed using a variety of morphometric procedures that utilize this geometry in their algorithms. For outlines, the coordinates can be studied themselves, or as part of a curve further quantified using techniques such as Fourier analysis. For studies using landmarks, the morphology of a specimen can be quantified as constellations of coordinate values for landmark points, and studied using Procrustes or other methods. Procrustes methods explore shape differences by reducing all specimens to an equivalent size; techniques vary, depending on the algorithm used and how size is defined.

Morphospaces and unique approaches

Morphospaces are multidimensional entities, first developed by Raup (1966), where each axis is defined by a different component of shape. Empirical morphospaces are built from measured data by using axes based directly on shape variables, and plotting real organisms inside this space. Theoretical morphospaces use mathematical functions to generate forms that resemble real organisms. The goal of such theoretical constructions is to

compare real data within a wider, hypothetical framework of 'constrained possibilities' defined by the functions employed to simulate the morphologies. Definition of morphospaces allows researchers to compare the dispersion of groups within them, often with a time component, and interpret these results within phylogenetic and functional contexts (Fig. 5.1.1.1). Evaluating regions of morphospace that remain unexplored can provide an insight into the constructional limitations and biology of the organisms under investigation.

The classic application of this exploratory technique is to the morphospace of coiled organisms with accretionary growth (e.g. ammonites) which can be modelled as a logarithmic spiral. Logarithmic patterns in nature have been studied extensively by scientists for centuries but this work was elevated to more rigorous levels by developing four parameters that allowed such growth patterns to be summarized, compared, and graphically reconstructed (Raup 1966) (Fig. 5.1.1.2). Subsequent researchers have modified and studied the interrelationships of these parameters, and developed others. Among the various organisms that have been analysed in this way are gastropods, coiled cephalopods, foraminifera, brachiopods, and ungulates (horns).

Fractal geometry and cellular automata are also modelling tools that can be applied to study ontogenetic growth and the generation of stable patterns. Fractal geometry allows the modelling of development systems, especially in branching forms, using the property of self-similarity. Cellular automata are discrete, dynamic systems that can model development using individual components, called cells, that change their state in response to environmental feedback, including the state of neighbouring cells, following defined sets of rules. Colonial and/or modular organisms provide additional challenges and opportunities. Here, the shape of individual units can be described using standard methods, with an additional component describing the nature of the modularity (Harper *et al.* 1986).

Allometry and conventional approaches

Allometry is the study of size and its consequences. Although a variety of techniques can be used, allometry is most commonly studied in bivariate space, comparing the relative growth rates of pairs of structures. Morphology is summarized by the slope and intercept of lines which fit the bivariate data; these parameters are then compared for different groups (Fig. 5.1.1.3). Slopes significantly different from unity indicate that one structure is growing at a much faster rate than the other. Lines

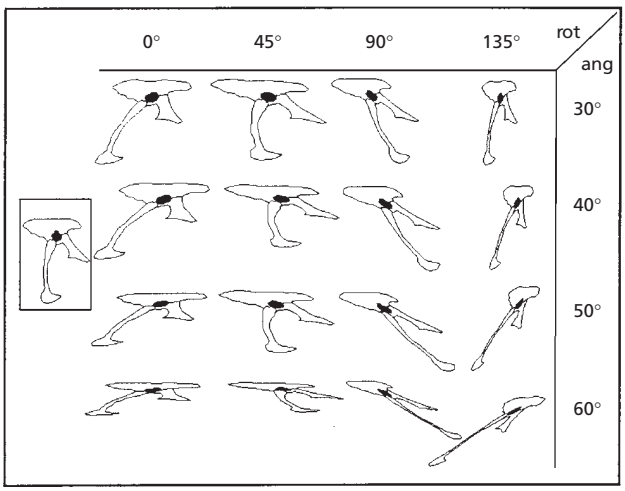


Fig. 5.1.1.1 Morphospace generated by applying successive uniform transformations to the *x*- and *y*-coordinates of the left-lateral view of the hip of the dinosaur *Deinonychus antirrhopus*, shown inside the box. This morphospace represents the 'possibilities of change' given a set of initial conditions (the original *x*- and *y*-coordinates), a set of boundary conditions (the parameters ang, a rough measure of the magnitude of the transformation, and rot, the original position from which the transformation is made, both given as angles and measured in degrees), and the constraints imposed by the properties of the uniform function. Each column can be interpreted as a different morphological trend; thus, column rot = 90° shows a mathematical trend that models the retroversion of the pubis seen in the dinosaur–avian transition. (Redrawn from Rasskin-Gutman and Buscalioni 1996.)

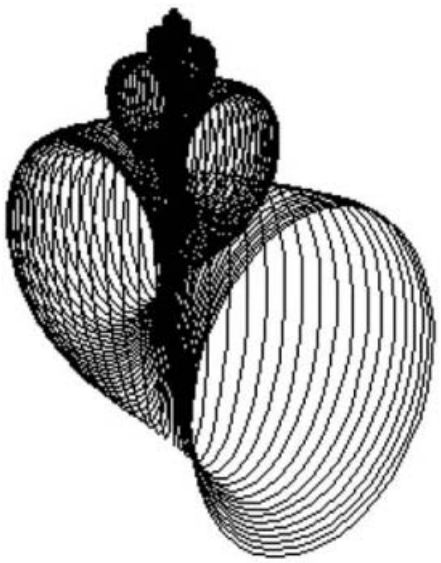


Fig. 5.1.1.2 Reconstruction of a gastropod, using Raup's (1966) four parameters to describe shell coiling: apertural shape, whorl expansion rate, translation rate, and displacement rate. An additional value was used to define the angle between the major axis of the aperture and the coiling axis.

with non-zero intercepts produce shape changes with increase in size.

Historically, shape has usually been summarized using ratios: the value of one measurement divided by that of another, often a standard size estimator such as total length. As such, ratios are used to provide an estimate of shape independent of size, making different specimens more comparable. This is most commonly done to discriminate between different taxa or morphs. However, ratios can be problematic because most growth curves do not have zero intercepts and, consequently, the ratio of a pair of measurements will frequently change greatly throughout growth, even for a single taxon. Different groups can also share the same ratios at different parts of their ontogenies. Ratios are increasingly being replaced by more standard bivariate allometric analyses, which can supply more useful information.

In most conventional studies, morphologies are represented by a series of measurements (variables) for a group of specimens and contained in a data matrix. Multivariate methods, such as Principal Components Analysis, have been developed to reduce this multidimensional data to a smaller number of axes, each a combination of the original variables. Typically, one of these new axes will represent size, and the value (score) for each specimen on it will be a multivariate estimate of its overall size. Other axes will represent morphological differences that are not size related, e.g. taxonomic differences, sexual dimorphism (Fig. 5.1.1.4) (Chapman *et al*. 1981).

Another way that palaeontologists quantify morphology is through codification, i.e. developing categories of morphologies and noting the distribution of taxa among these groupings. This is the basis for developing morphological data matrices for phylogenetic analysis and has been used extensively with most major groups of taxa. Binary codification (0,1; where 0 represents generally a 'primitive' state for a character and 1 represents any other 'derived' state) has been favoured in cladistic analyses, although multistate and continuous characters are also used and are the subject of much ongoing development.

Morphological quantification is also the basis for many other important areas of inquiry in palaeontological research. For example, three-dimensional modelling is an abstraction of a fossil structure in terms of coordinates taken directly from the specimen. Using computers, these models can be animated in virtual space for functional analyses. Also, prototypes (three-dimensional hard-copies) can be generated for further research using more direct manipulation.

Conclusion

Clearly, the quantification of morphology is a required step in the development of more rigorous research in the science of palaeontology. Fossils provide a vast amount of morphological data that must be reduced to a man-

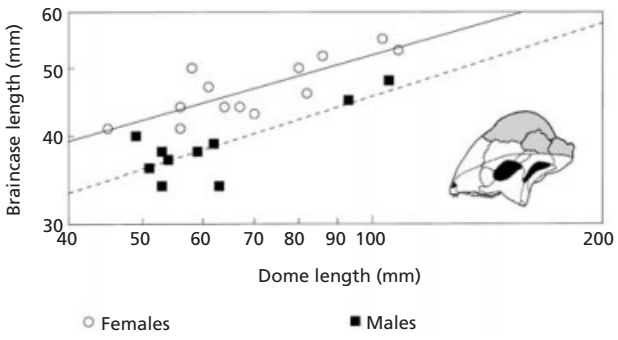


Fig. 5.1.1.3 Bivariate allometric analysis of the cranial dome vs. braincase length of the pachycephalosaurid dinosaur *Stegoceras* using logarithms of the original data (Chapman *et al*. 1981). The relatively flat slopes, both less than 0.35, indicate that the dome had a growth rate far exceeding that of the braincase. A difference in the *y*-intercept value separates the sexes; it produces a much larger dome in the presumed males for any given braincase size (evident by tracing a horizontal line on the graph). The cranial dome is a dimorphic structure apparently used for some type of social combat.

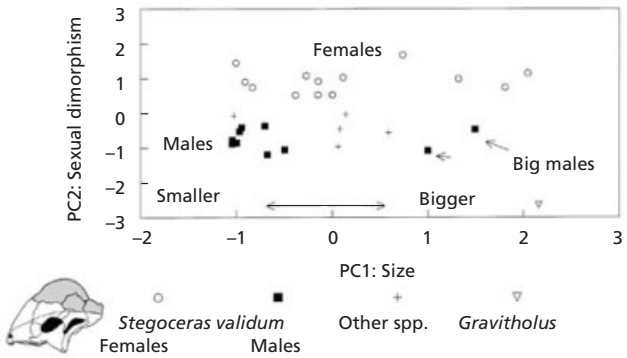


Fig. 5.1.1.4 Principal Components Analysis (PCA) of 15 skull, dome, and braincase measurements for *Stegoceras*. The *x*-axis represents size (PC1): the greater the value, the larger the specimen. The *y*-axis (PC2) reflects sexual dimorphism in *S. validum* and is defined by variation in braincase size relative to dome size. The supposed females, with higher values for the *y*-axis, have larger braincase sizes for a given dome size. Note that PC1 shows that there is no sexual size dimorphism apparent in the data, i.e. females attain overall sizes as large as males. Note that the specimen of the pachycephalosaurid *Gravitholus*, included for comparison, is widely separated from those of *Stegoceras*. (Redrawn from Chapman *et al*. 1981.)

ageable size for analysis. Theoretical morphology, the general framework for quantifying morphology, allows these data to be extracted, simplified, and studied in a biologically meaningful way.

References

Bookstein, F.L. (1991) *Morphometric tools for landmark data: geometry and biology*. Cambridge University Press, New York.

Chapman, R.E., Galton, P.M., Sepkoski, J.J. Jr and Wall, W.P. (1981) A morphometric study of the cranium of the pachycephalosaurid dinosaur *Stegoceras*. *Journal of Paleontology* **55**, 608–618.

Harper, J.L., Rosen, B.R. and White, J., eds. (1986) *The growth and form of modular organisms*. The Royal Society, London.

Rasskin-Gutman, D. and Buscalioni, A.D. (1996) Affine transformation as a model of virtual form change for generating morphospaces. In: L.F. Marcus, M. Corti, A. Loy, D. Slice and G. Naylor, eds. *Advances in morphometrics*, pp. 169–178. Plenum Press, New York.

Raup, D.M. (1966) Geometric analysis of shell coiling: general problems. *Journal of Paleontology* **40**, 1178–1190.

Thompson, D'A.W. (1917) *On growth and form*. Cambridge University Press, Cambridge (2nd edn, 1942).

5.1.2 Morphometrics and Intraspecific Variation

N.C. HUGHES

Introduction

Traditionally, fossil species have been diagnosed using specific morphological characters purportedly restricted to discrete stratigraphic intervals. As interest has grown in using fossils to address evolutionary questions, alternative approaches have been applied to assess variation in fossil form; emphasis has shifted from the recognition of key stratigraphically specific characters to understanding patterns of covariation among attributes. The best medium for accessing covariation is provided by morphometrics (see Section 5.1.1). Morphometrics are particularly valuable for studies conducted at low, as opposed to higher, taxonomic levels because sample-wide homology of attributes selected for analysis can be more confidently assumed. As in cladistic methods in systematics, attributes for morphometric analysis are selected explicitly, so that the results are both easily interpretable and testable.

There are two fundamental aspects of the morphometric analysis of intraspecific variation in fossils: (1) the recognition of discrete morphotypes; and (2) documenting patterns of variation within and among morphotypes. Most species considered in palaeobiology are morphospecies, defined using the premise that distinct morphotypes (groups of phenetically similar individuals) represent different taxa. This restriction to phenotypic morphology, without any direct information about genotype, likely limits the species-level resolution of palaeobiological studies in some cases. Polytypic species are common in extant clades, and therefore distinct morphotypes do not always represent distinct species. Likewise, several sibling species might constitute a single morphotype. In the fossil record, information on organismal biology and geological occurrence can help resolve the species identities in some of these cases. For example, two distinct morphotypes with common stratigraphic and geographical ranges may sometimes be interpreted as sexual dimorphs. Given these problems, rigorous description of the continuity of morphological variation is essential before the relationships between morphotypes and species can be explored.

Recent advances have significantly refined the discriminatory power of morphometric techniques. When these improvements have been applied to studies of extant coral and bryozoan taxa, encouraging congruence has been revealed between species defined by independent morphometric and genetic criteria (Jackson and Cheetham 1994). This offers the promise that groups identified using appropriate morphometric techniques may often constitute biospecies. Furthermore, even when the relationship between morphotypes and species remains in doubt, patterns of variation within and among morphotypes retain intrinsic biological significance, independent of species definition. For example, it may never be possible to determine the exact number of species present within a fossil morphotype showing continuous but clumped variation. Nevertheless, this pattern contains information about genomic controls operative at low taxonomic levels within this taxon and about its ecological structure.

There are several styles of intraspecific variation, including growth-related shape change (allometry) various kinds of asymmetry, polymorphism, and ecophenotypic variation. Morphometrics provides tools which help to identify these different styles, and the contribution of each style to the overall pattern of intraspecific variation. This approach is particularly valuable for assessing the degree to which different patterns of phenotypic variation are integrated or constrained within morphotypes.

Quantitative attributes of intraspecific variation

Many morphometric analyses of fossil species are based on linear distances measured between morphological landmarks considered to be homologous throughout the sample. In some cases information on angular relationships and codings for multistate characters are also included. Matrices of these data are then examined synoptically to detect common patterns of variation. In the case of bivariate datasets various forms of regression analysis are used, and Principal Components Analysis (PCA) is often applied to multivariate datasets (see Section 5.1.1).

Graphs showing the distribution of individuals in a morphological space or 'morphospace' are an effective way of presenting the results of a study. Axes can be metric dimensions (e.g. Fig. 5.1.1.3), or multivariate axes summarizing overall patterns of morphological variation (e.g. Fig. 5.1.1.4). The distribution of individuals gives an immediate impression of the manner of morphospace occupation; subclusters within overall trends suggest that more than one morphotype is present in the sample. Other statistics can then be employed to evaluate the significance and degree of variation within morphotypes. Measures of correlation help us to determine the way in which attributes covary within the sample, and the relative significance of particular styles of variation. This information can be used to determine whether the controls of morphological variation within a sample are complex and mosaic, or whether they represent a small number of simple underlying themes.

Techniques based on linear distances between homologous points are now commonly referred to as 'traditional' morphometrics. An inherent disadvantage of these techniques is that the resultant patterns of variation are conceptually difficult to relate to the original specimens, because it is difficult or impossible to recreate the original geometry of the specimen from abstracted matrices of linear measures. In contrast, geometrical morphometric approaches (Rohlf and Marcus 1993) can provide results that are intuitively appealing because they are based on the geometrical relationships among key morphological points, known as landmarks, which in the case of intraspecific studies can be considered homologous throughout the sample (Fig. 5.1.2.1a).

Procrustes methods superimpose landmarks for series of specimens (Fig. 5.1.2.1b). This provides a visually appealing summary of both the overall degree of intraspecific variation and its localization to particular landmarks. Procrustes fits can also be useful in demonstrating ontogenetic differences in relative proportions between specimen pairs (Fig. 5.1.2.1c). Degrees of intraspecific variation can be compared on the basis of variation of specimens about the mean form for a mor-

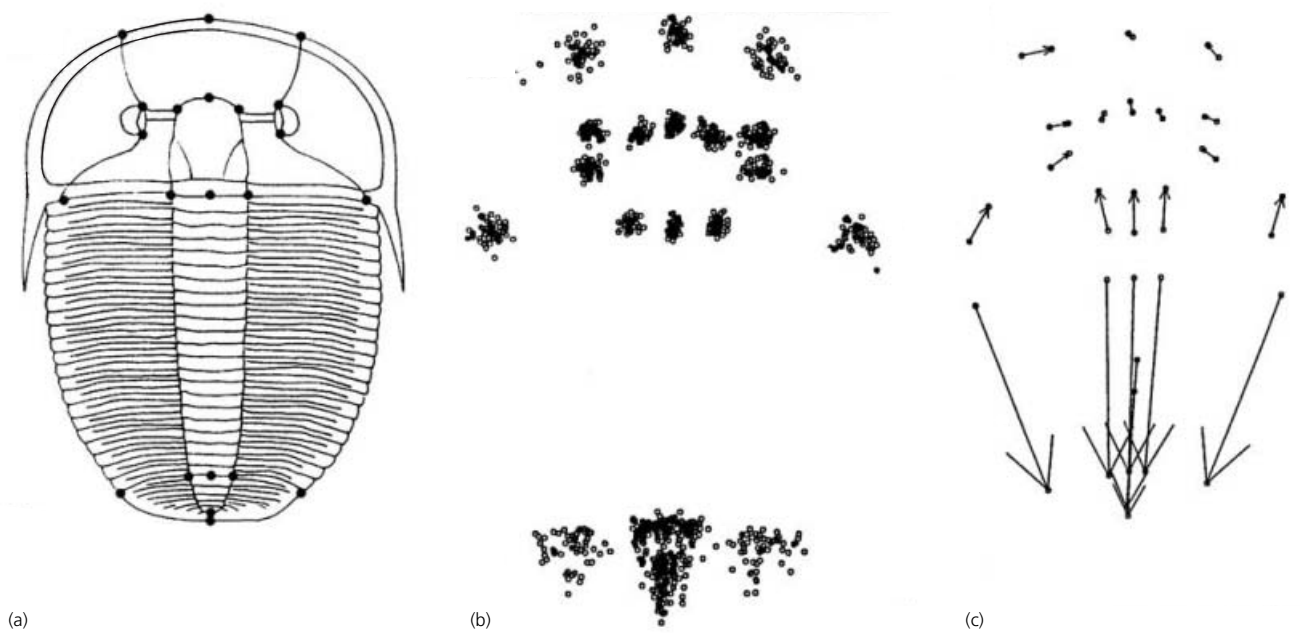


Fig. 5.1.2.1 (a) Twenty-two morphological landmarks defined on the dorsal exoskeleton of the Silurian trilobite *Aulacopleura konincki*. (b) Superimposition of adult specimens of *A. konincki*, illustrating degree and localization of variation. (c) Vector plot showing ontogenetic shifts in relative positions of landmarks between a small preadult and a large adult *A. konincki*. (See Hughes *et al*. 1999.)

photype, and interspecific distances by computing the distance between mean forms. The Thin Plate Spline technique (Bookstein 1991) takes geometrical morphometrics a step further by identifying series of localized, mutually independent, patterns of shape variation. This forms the geometric complement to correlation analyses in traditional morphometrics, but one that can be readily expressed in terms of the geometrical movement of landmarks.

Applications of intraspecific variation

Intraspecific variation is central to evolutionary biology because it is a basic source of evolutionary pattern. Defining and interpreting morphotype boundaries is not only an important first step in evolutionary analyses, but the process may itself reveal important information on the nature of biological entities. Application of landmark-based techniques to the pelagic foram *Globorotalia* shows that the boundaries between forms traditionally recognized as discrete morphospecies are considerably less clear than was previously assumed (Tabachnick and Bookstein 1990). A similar pattern has now been found in a variety of other groups, including trilobites and ammonites.

Ontogenetic studies of individual taxa and of groups of individuals provide important insights into both patterns of phenotypic variation within species, and possible evolutionary relationships among species. For example, ontogenetic studies form the basis for inferring patterns of change in developmental rate timing (heterochrony; see Section 2.3.5) or in spatial positioning of development (heterotopy). In heterotopy evolutionary change occurs in the area influenced by particular developmental patterns, whereas in heterochrony changes are restricted to the timing of expression of developmental patterns, operative in similar spatial domains.

The value of palaeontological evidence in debates concerning the tempo and mode of speciation depends directly on the ability to contrast levels of intraspecific variation with interspecific distances, as shown in studies of Neogene bryozoans (Jackson and Cheetham 1994 and references therein). In this case, intraspecific variation within the genus *Metrarabdotos* proved minor compared to distances between taxa, suggesting relatively rapid shifts in morphology associated with speciation events against a background of intraspecific stasis. This pattern extends to other genera, and provides some of the best examples of punctuated evolution in the fossil record.

Trends in intraspecific variability across broad stratigraphic intervals are important because they may indicate underlying controls on patterns of evolution. Quantitative analyses of the range of intraspecific variation in a number of trilobite taxa have concentrated both within a single Cambrian stage, and over the interval of the Early Cambrian to the Middle Silurian. Although no obvious overall trend in intraspecific variability emerged at either scale, it is clear that individual taxa may show strikingly different degrees of intraspecific variation, even within close ecological associations. A promising way forward is to determine the extent to which patterns of variation are determined by phylogenetic or 'internal' constraints, as opposed to ecological or 'external' controls. To do this requires mapping of the phylogenetic context of levels of intraspecific and interspecific variation, and resolving the ecological context of these patterns. Such an approach has been applied to the magnitude of transitions between sister species in early Palaeozoic gastropods (Wagner 1995) and suggests that increasing phylogenetic constraint occurred over this interval. This indicates that a rapid initial diversification of gastropods may have been fuelled by large morphological transitions among early species. Similarly, the relationship between variation in overall shape and the development of basic aspects of body plan can provide insights into basic developmental controls in fossil groups, such as the generation of segmentation pattern (Hughes *et al*. 1999).

References

Bookstein, F.L. (1991) *Morphometric tools for landmark data: geometry and biology*. Cambridge University Press, New York.

Hughes, N.C., Chapman, R.E. and Adrain, J.M. (1999) The stability of thoracic segmentation in trilobites: a case study in developmental and ecological constraints. *Evolution and Development* **1**, 24–35.

Jackson, J.B.C. and Cheetham, A.H. (1994) Phylogeny reconstruction and the tempo of speciation in cheilostome Bryozoa. *Paleobiology* **20**, 407–423.

Rohlf, F.J. and Marcus, L.F. (1993) A revolution in morphometrics. *Trends in Ecology and Evolution* **8**, 129–132.

Tabachnick, R.E. and Bookstein, F.L. (1990) The structure of individual variation in Miocene *Globorotalia*. *Evolution* **44**, 416–434.

Wagner, P.J. (1995) Testing evolutionary constraint hypotheses: examples with early Paleozoic gastropods. *Paleobiology* **21**, 248–272.

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5.1.3 Disparity vs. Diversity

M.A. WILLS

Introduction

Diversity

Mass extinctions, radiations, competitive interactions, and the effects of ecological change have all been studied with reference to turnover in numbers of families, genera, and species (see Section 2.4 and references therein). The differential effects of major extinction events on groups progressively further up the taxonomic hierarchy are well documented. Species and genera may be wiped out with relative ease. However, extinguishing a family often entails knocking out tens or even hundreds of genera, and the demise of an order implies the loss of many families. In general, as the hierarchical level considered increases, perturbations in taxonomic diversity through time decrease.

Disparity

In contrast to diversity, disparity refers to the morphological variety exhibited by a group of taxa. The taxonomic diversity of a highly disparate group can be comparatively low. Disparity usually correlates more closely with numbers of higher taxa (orders, classes, and phyla) than with numbers of species (Gould 1989). However, disparity is not equivalent to higher taxonomic diversity, because taxonomic status does not imply any particular level of morphological distinctiveness.

The disparity of a randomly chosen fish, an arthropod, and a worm will be greater than that of three species of mammal (however, selected) using almost any set of morphological characters. Modern coelacanths and horseshoe crabs are lone representatives of what were once vastly more diverse clades, higher taxa, and body-plan designs. The demise of either of these 'living fossil' groups would be more significant than the extinction of, say, a genus of gobies or three genera of spiders, precisely because their contribution to modern disparity is greater.

There are no standard sets of measurements for assessing morphological variety or disparity. Indices must therefore be understood in the context of some particular aspects of form, or the sets of characters used to represent them. Estimates of disparity for the same taxa, derived from different datasets, may vary. However, in some respects this is analogous to the potential incongruences between cladograms inferred from different character sets. Where workers studying different aspects of form reveal similar patterns, confidence in the biological validity of the results is reinforced. Where patterns differ, the conflict may itself be informative.

Quantifying disparity from cladograms

A phylogenetic index of disparity can be derived from the number of character state changes subtended by a clade or group of interest on a given tree (Wills *et al.* 1994). An alternative approach records the number of nodes subtended (Smith 1994). A more refined index measures the mean character distance (through the cladogram) divided by the number of intervening branches (e.g. two branches for sister taxa) for all possible taxon pair comparisons in a group. This approximates the mean number of character state changes between all adjacent pairs of taxa, whether real (terminals) or hypothetical (internal nodes).

Phylogenetic estimates are predicated on a given cladogram (which may be incorrect). They approximate the gross amount of morphological change taking place in the evolution of a group, including character reversals. Phylogenetic estimates may be particularly useful in inferring evolutionary mechanisms. Phenetic indices of disparity attest to net differences in morphology, and are determined by the ultimate (or end-point) distributions of taxa, irrespective of their evolutionary trajectories. Comparisons of cladistic and phenetic distances may suggest the existence of evolutionary constraints.

Phenetic indices of disparity

There are many methods for measuring disparity phenetically (e.g. Wills *et al.* 1994). Approaches differ principally in three respects: (1) the variables used to quantify morphology; (2) how variables are combined; and (3) the index of dispersion used.

Quantifying morphology

Measuring morphological differences (like inferring phylogeny) requires that taxa are referred to a common set of descriptors. Studies on different groups usually require distinct character sets (the same set of descriptors could not be used to study dinosaurs and dinoflagellates). For this reason, disparity indices only attest to relative differences between groups.

A distinction can be drawn between methods that quantify shape or shape change directly (morphometrics), and those that represent aspects of form as discrete characters. Both approaches may or may not include information on biological homology. Morphometric methods include techniques that use landmark reference

points (e.g. interlandmark distances, Procrustes distances, and partial warps), and those that describe curves, outlines, or surfaces (e.g. Fourier and eigenshape analysis) (see Section 5.1.2). These all yield distances and coefficients that can be used as variables. Traditionally, workers have strongly advocated the use of either landmark or outline descriptions, but some analyses now combine both approaches. Landmarks can represent biologically homologous points (e.g. extremes or conjunctions of homologous structures) or merely geometrically homologous references. Data from geometrical landmarks, along with those from outlines, are perhaps most useful for studies of functional morphology.

Morphometric methods may be most appropriate for studying the least dissimilar morphologies (e.g. species within genera). When attempting to analyse higher taxa (e.g. different orders and classes), only a degenerate set of references are likely to be found (particularly biological landmarks), and outlines may be increasingly difficult to interpret. Much variation will be overlooked unless discrete characters are used (either alone or in conjunction with landmark data) (Wills 1998).

Combining variables

Variables are usually combined to produce some form of morphospace, within which the most similar taxa plot close together, and the least similar farthest apart. Empirical morphospaces are usually characterized as those whose parameters are determined *after* observation or measurement of specimens. The parameters of theoretical morphospaces are determined *a priori*, and only then are real taxa located within them.

A common approach in empirical studies is to refer taxa to a small number of uncorrelated (orthogonal) principal component or coordinate axes (an ordination). Taxa can be ordinated in a variety of ways (Wills *et al.* 1994; Wills 1998) depending on the nature of the data, and the questions being addressed. The first axis expresses the greatest portion of the variance, the second the next, and so forth. Two advantages ensue: (1) a large proportion of the total variance can often be visualized in a two- or three-dimensional scatter plot; and (2) large-scale covariation between variables is factored out. Figure 5.1.3.1 illustrates a three-dimensional morphospace plot for fossil and Recent arthropod genera. Three coordinates encompass 38% of the variance in the original 97 two-state characters.

Indices of disparity

Figure 5.1.3.1 reveals that: (1) most arthropods lie in three broad regions of the morphospace; and (2) some groups cluster more tightly than others (the atelocerates are less scattered than the arachnomorphs and crustaceans). A simple index of disparity counts the number of arbitrarily sized (here 0.5 axis units on each side) morphospace squares or boxes occupied by each group of interest. Atelocerates occupy 8 squares, crustaceans 12, and arachnomorphs 14.

A more refined method operates by placing a single box around all members of the group. Its area or volume is calculated by multiplying the lengths of the sides. Hypervolume calculations can be extended into n dimensions, although products are usually expressed as the nth root. The number of dimensions included is arbitrary. Later axes are increasingly less significant, but have equal weight in the calculations. An arbitrary compromise is often to use sufficient axes to capture 90% of the total variance (25 out of 46 for the arthropods). Skree plots (graphing the magnitude of eigenvalues against components, with the retention of factors above the inflection point in the slope) are among the alternatives (Wagner 1995). Another distinct approach is to add the lengths of the sides. Additive indices allow axes to contribute roughly in proportion to their variance and importance, so the precise number incorporated is less critical (Wills 1998).

The 'boxing' method provides estimates of the total *range* of morphology. The dimensions of the box are defined by the most eccentric points on a given set of axes. Outliers can hold the morphospace envelope open, and range-based indices are insensitive to the distributions of points within the boxes. Range-based indices are therefore unperturbed by inconsistencies of taxonomic splitting, but are more sensitive to the number of taxa within groups (both properties may be desirable, but see comments on rarefaction below). An alternative is to investigate the variances of the scores of taxa on each axis (Foote 1991, 1993). This is simply given by the mean squared difference between each score and the average score. Taxa defining a box will have a low variance if many of them are bunched at its centre, and a higher variance if they are widely scattered or congregate at its edges. Variances (like ranges) can be multiplied or added, with similar consequences. Variances indicate the average dissimilarity between forms, and are relatively insensitive to the presence or absence of rare and eccentric body plans.

Other indices of disparity operate by measuring the mean distance of a group of taxa from its own centre of gravity, mean morphology, or centroid (Table 5.1.3.1 and Fig. 5.1.3.2). The centroid for all of the taxa in a centred ordination is the origin (Figs 5.1.3.1 and 5.1.3.2). The centroid for subgroups may lie close to the overall centroid (where groups are broadly overlapping), or far from it. In the arthropod example, the three main groupings (arachnomorphs, crustaceans, and uniramians) have local centroids far from the overall origin, since they occupy distinct regions of the morphospace. A similar

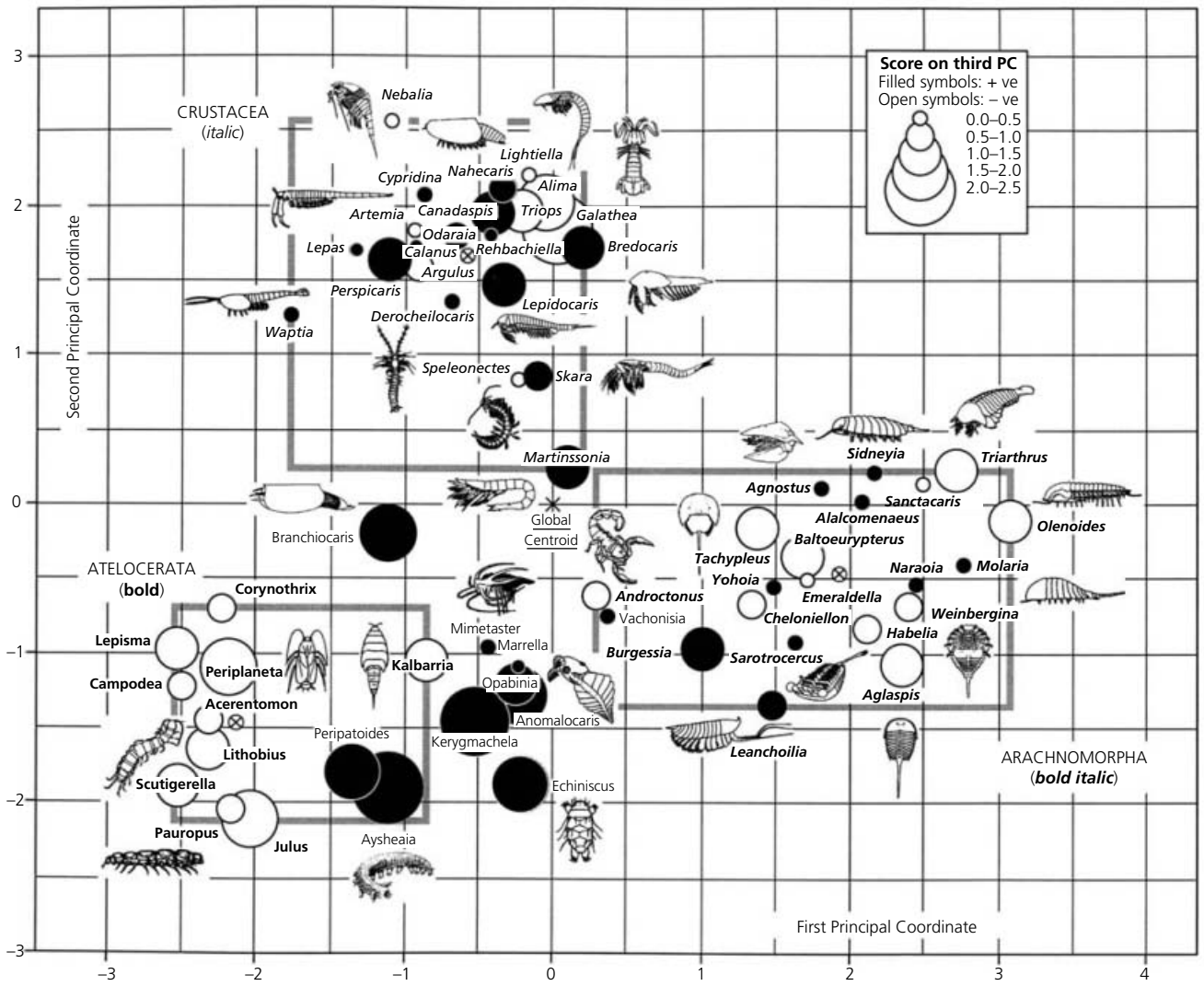

Fig. 5.1.3.1 Principal Coordinates Analysis of fossil and Recent arthropods. Third coordinate normal to the plane of the page. Positions of icons very approximate. Subgroup centroids for atelocerates, crustaceans, and arachnomorphs indicated by crossed circles. A simple index of disparity in two dimensions for the three major arthropod groups is illustrated (area of grey boxes). Atelocerates occupy 3.3 square axis units, crustaceans 4.5, and arachnomorphs 4.4. Based on an analysis by Wills *et al.* (1998).

approach measures the mean distance of every taxon in a group from every other in the same group (Wills *et al.* 1994) (Table 5.1.3.1 and Fig. 5.1.3.2). Intertaxon and centroid-to-taxon distances are independent of the axes of the morphospace. Another axis-independent approach is to calculate the volume or hypervolume of a convex hull (a polyhedron or hyperpolyhedron) uniting all outermost points. This also represents a refinement on the use of hyperboxes.

The contribution that a subgroup of taxa makes to total disparity is proportional to the average squared Euclidean distance of its points from the overall centroid (not the subgroup centroid) (Foote 1993). An alternative method is to compare the disparity of a group to its disparity with a certain subgroup omitted. If the resulting disparity differs substantially from the original disparity, then the subgroup in question has a significant effect on the overall total.

Morphological rarefaction

Larger subgroups of taxa might be expected to exhibit a greater *range* of morphologies than smaller ones, simply because there are more points to be scattered in the morphospace. In Fig. 5.1.3.2(a) the larger group (A, with six taxa) is more disparate than the smaller (B, with four taxa), but we do not know if this is purely a sample size effect. Similarly, the disparity of the 10 atelocerates in

Table 5.1.3.1 Several indices of disparity for the three main arthropod groups in Fig. 5.1.3.1. The second and third rows are derived from the projection of taxa on to the first two principal coordinates of Fig. 5.1.3.1. The remainder are based on the scores of taxa on the first 25 principal coordinates (encompassing approximately 90% of the total variance).

Group	Atelocerata	Crustacea	Arachnomorpha
Number of genera (n)	10	22	20
Number of arbitrarily sized, 2D boxes occupied	8	11	14
Product of ranges on first two principal coordinates	3.341	4.457	4.437
Sum of ranges	33.861	50.185	58.015
Product of ranges	404	8 345 856	616 863 600
Product of ranges (25√)	1.271	1.892	2.247
Rarefied sum of ranges (jackknifed to $n = 10$)	33.861	40.911	48.678
Rarefied product of ranges (jackknifed to $n = 10$)	1.271	1.532	1.880
Sum of variances	5.042	7.600	10.143
Product of variances	9.34E–21	1.56E–16	3.25E–12
Product of variances (25√)	0.158	0.233	0.347
Mean Euclidean distance from subgroup centroid	2.183	2.720	3.165
Mean Euclidean distance between all taxa in subgroup	3.186	3.917	4.566
Relative contribution of subgroup to total disparity	13.364	10.777	14.202

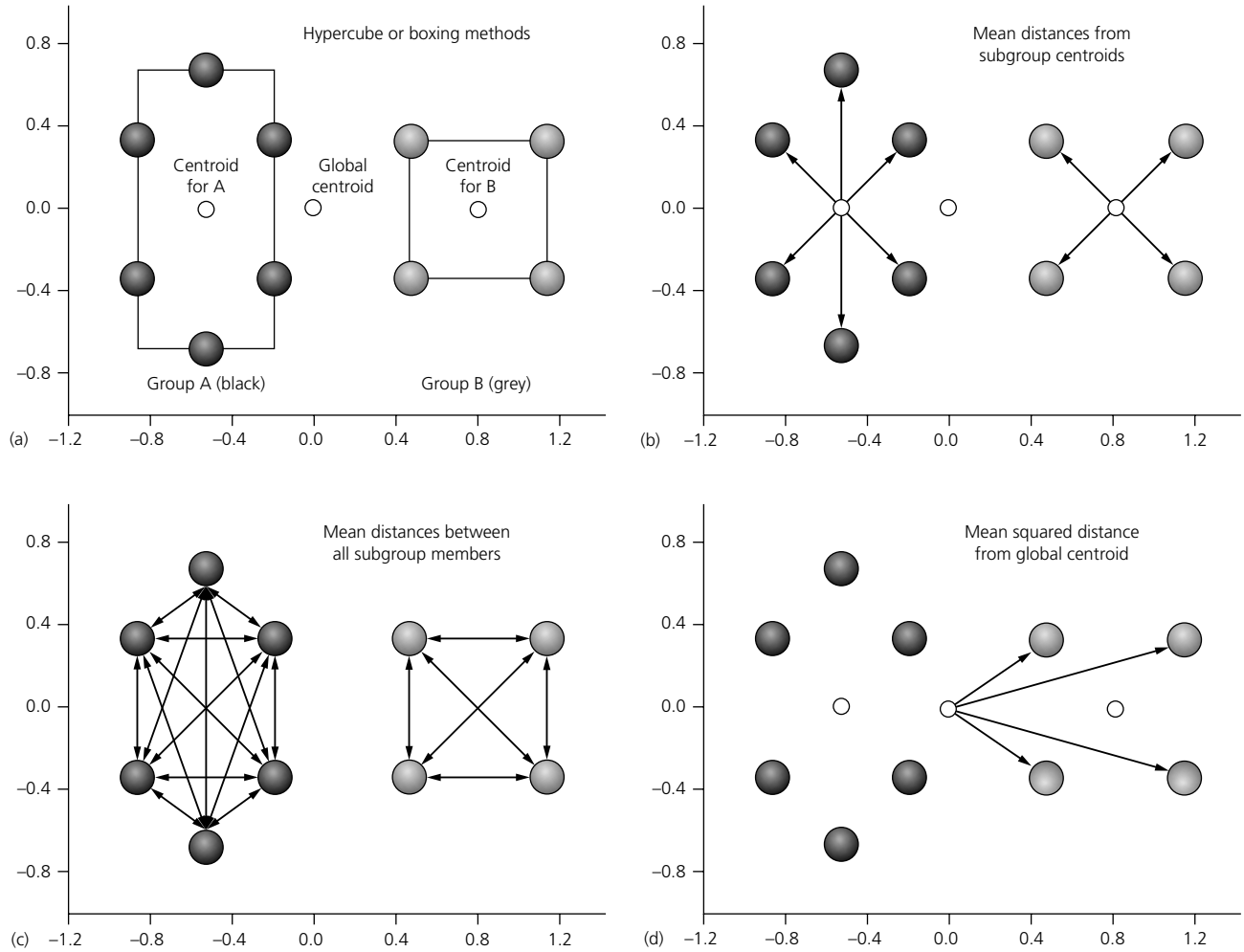

Fig. 5.1.3.2 Some indices of disparity for subsets of taxa (groups A and B) in a single analysis. (a) The use of hypercubes containing all the points in each subgroup; subgroup centroids always lie within these boxes, but not necessarily at their centres (as in this example); the global centroid may lie outside all the hypercubes; disparity can be calculated as the product or sum of the lengths of the sides of the hypercubes. (b) Disparity for subgroups A and B calculated as the mean Euclidean distance from their respective group centroids. (c) Disparity for subgroups A and B calculated as the mean Euclidean distance between all possible pairs of taxa in each subgroup. (d) The contribution of group B to total disparity (group A plus group B) is proportional to the average squared distance of all points in group B from the global centroid (not the centroid for group B).

Fig. 5.1.3.1 is less than the disparity of the 22 crustaceans (Table 5.1.3.1). Rarefaction attempts to address this by repeatedly (e.g. 1000 times) pulling smaller subsamples from the larger group (in this case, samples of 10 from 22), and recalculating the disparity each time. [Resampling can be with replacement (bootstrapping) or without it (jackknifing).] This yields a mean, with approximate confidence intervals. In the arthropod example, the atelocerates have lower range sums and products than the crustaceans, even after correcting for sample size differences.

Patterns of disparity through time

Intuitively, clades might be expected to explore morphospace progressively through time, radiating away from a single point (the common ancestor). However, studies on a number of clades indicate that groups often explore morphospacial extremes very early in their history, e.g. Palaeozoic blastozoans, bryozoans, and gastropods (Wagner 1995), Palaeozoic and Mesozoic crinoids, Cambrian marine arthropods (Wills *et al.* 1994), Ordovician trilobites, and angiosperms. Subsequent evolution frequently serves to fill in gaps and revisit previously occupied areas (reversals). In fact, disparity can often peak much *sooner* than diversity.

The disparity of trilobites through the Palaeozoic has been traced by considering groups of fossils in 'time slices' (Foote 1991). In this case (an exception) taxonomic diversity peaked in the Cambrian, but disparity peaked *later*, in the Ordovician (Fig. 5.1.3.3a). The Early Carboniferous saw a marked disparity crash, and by the end of the period the group occupied just a small pocket of morphospace, prior to its extinction at the Permo-Triassic boundary. Another study traced the fortunes of crustaceans (Wills 1998). Fossils from the Lower Cambrian filled approximately one-third of the morphospace occupied by their Recent counterparts. By the Upper Cambrian, this fraction exceeded a half. A drop in the Early Ordovician was followed by an irregular increase to near Recent levels by the end of the Carboniferous (Fig. 5.1.3.3b). The Ordovician to Permian reduction of trilobite disparity may be linked to the corresponding rise of the Crustacea (particularly the Eumalacostraca, which, like the trilobites, were predominantly benthic scavengers and predators).

Disparity and the Cambrian explosion

It has been claimed that problematic arthropod fossils from the Middle Cambrian Burgess Shale were vastly more disparate than the whole of the modern arthropod fauna (Gould 1989). This would have implications for the size of the apparent Cambrian 'explosion', the amount of evolution implied, and the overall 'shape of Life'. An ordination similar to that in Fig. 5.1.3.1 was used to investigate this claim (Wills *et al.* 1994). Many of the indices discussed above demonstrated comparable levels of disparity for Cambrian and Recent taxa (Table 5.1.3.1). A similar result has been shown for priapulids

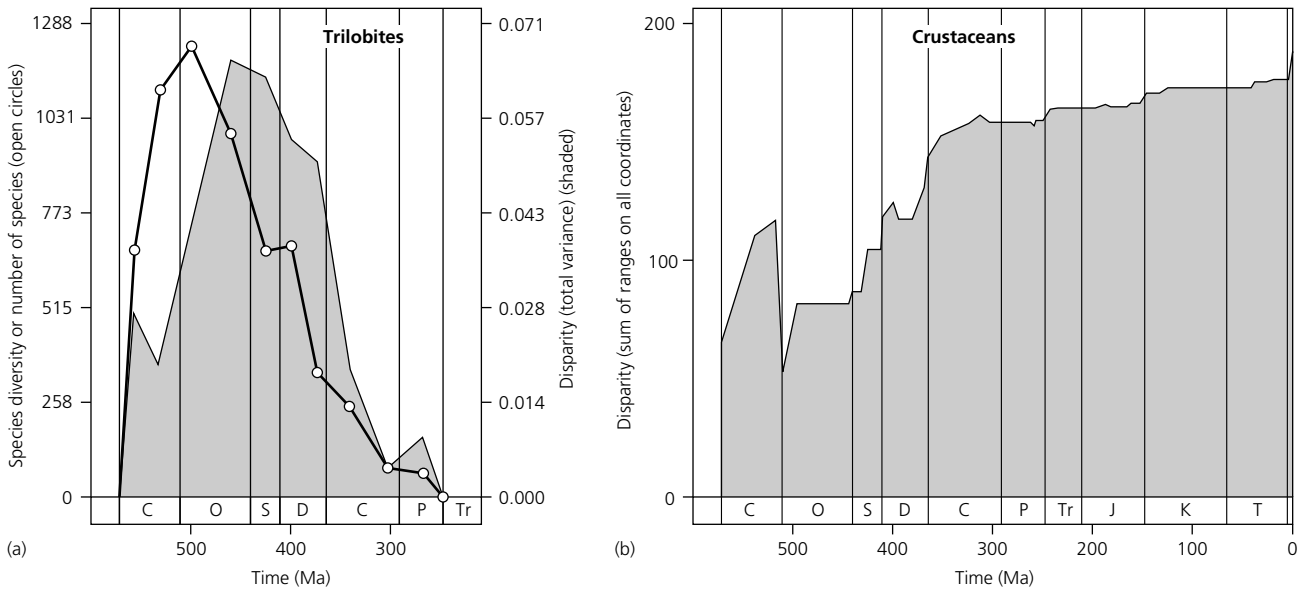

Fig. 5.1.3.3 (a) The diversity (open circles) and disparity (shaded) of trilobites through time; trilobites are unusual, in that their disparity appears to peak *after* their diversity. (b) The disparity (sum of ranges on all principal coordinates) of observed crustacean lineages through time; if the group is a clade, its disparity provides an index of the net amount of morphological change occurring since its radiation from the common ancestor. (a, Redrawn from Foote 1993; b, modified from Wills 1998.)

(Recent genera are actually slightly more disparate) despite the vastly greater abundance of these worms in the Cambrian.

Conclusions

Much can be learned by assessing the disparity of groups through time, in parallel with investigations into their diversity and phylogeny. Disparity provides an index of aspects of the morphological differences between forms. It also offers an index of the amount of morphological change necessary to realize a given set of morphologies, either in a phenetic (net change) or phylogenetic (gross change, including reversals) context. Cladograms, although vital in systematics, do not provide the most efficient mechanism through which to summarize all aspects of a group's evolution. A study of the relationship between morphospace filling and taxonomic diversity may offer important insights into a variety of macroevolutionary processes (e.g. clade radiation, extinction selectivity, and evolutionary constraints).

References

Foote, M. (1991) Morphologic patterns of diversification: examples from trilobites. *Palaeontology* **34**, 461–485.

Foote, M. (1993) Discordance and concordance between morphological and taxonomic diversity. *Paleobiology* **19**, 185–204.

Gould, S.J. (1989) *Wonderful life: the Burgess Shale and the nature of history*. W.W. Norton, New York.

Smith, A.B. (1994) *Systematics and the fossil record: documenting evolutionary patterns*. Blackwell Scientific Publications, Boston.

Wagner, P.J. (1995) Testing evolutionary constraint hypothesis with early Paleozoic gastropods. *Paleobiology* **21**, 248–272.

Wills, M.A. (1998) Crustacean disparity through the Phanerozoic: comparing morphological and stratigraphic data. *Biological Journal of the Linnaean Society* **65**, 455–500.

Wills, M.A., Briggs, D.E.G. and Fortey, R.A. (1994) Disparity as an evolutionary index: a comparison of Cambrian and Recent arthropods. *Paleobiology* **20**, 93–130.

Wills, M.A., Briggs, D.E.G. and Fortey, R.A. (1998) Evolutionary correlates of arthropod tagmosis: scrambled legs. In: R.H. Thomas and R.A. Fortey, eds. *Arthropod relationships*, pp. 57–65. Chapman and Hall, London.

5.2 Calibrating Diversity

5.2.1 Estimating Completeness of the Fossil Record

M. FOOTE

Introduction: the nature of completeness

The incompleteness of the fossil record affects our view of evolution, so it is essential to understand the nature and magnitude of incompleteness and to correct for it. Any attempt to measure completeness requires a model of preservation. Longer-lived taxa are more likely to be preserved; thus, a model of evolution is often implicit as well. These models may seem burdened with unrealistic assumptions, but they are no more so than taking the fossil record at face value, which tacitly assumes a complete, or at least unbiased, record.

Two principal aspects of completeness need to be considered (Paul 1990): (1) the proportion of taxa preserved; and (2) the probability of preservation during specified intervals or moments within a taxon's lifetime. Incompleteness reflects both the fossil record itself and our knowledge of it, but these two factors can be difficult to distinguish in practice, and it may not be necessary to do so. Analysing the growth of palaeontological knowledge gives important insights into the robustness of evolutionary patterns, the practices of palaeontologists, and the geographical, stratigraphic, and taxonomic areas in special need of study. The treatment of data is the same, however, whether a species is unknown because it was never fossilized or because it was never discovered.

Species are more likely to be preserved if they are longer-lived, abundant, widespread, more robust structurally, and of more stable mineral composition. They are more or less likely to be known depending on peculiarities of palaeontological interest. Dinosaurs are more intensively studied than bryozoans, and fossiliferous strata are best known near academic institutions. For the sake of modelling, it is convenient to express these

complex factors in terms of the per-capita extinction rate q, which is the reciprocal of mean duration, and the per-capita preservation rate r, which entails the factors other than duration (Pease 1985; Foote 1997). Both rates can vary among taxa as well as over time. The net probability of preservation P_P expresses the likelihood that a taxon will be preserved at least once during its entire duration; for any group of taxa that are preservationally equivalent, this is the same as the proportion of taxa preserved. The probability of preservation at least once during a unit stratum or interval of time, denoted R, depends on r and the length of the interval. Also, if the taxon's true duration does not cover the entire interval, R depends on how much of the interval it is likely to span, which is a function of the origination and extinction rates.

These rates and probabilities are closely interrelated. As q increases (i.e. as taxonomic duration declines), R and P_P decline. Conversely, R and P_P increase along with r. Given the opposing effects of extinction rate and preservation rate on completeness, the ratio between these rates is a useful, dimensionless number. When the rates are constant and when the total span of time under study is very long relative to taxon durations, the proportion of taxa preserved depends only on the ratio r/q (Fig. 5.2.1.1). Moreover, if interval length is expressed as a multiple of $1/q$ (i.e. as a multiple of mean taxonomic duration, a natural time scale for a number of palaeobiological problems), then the probability of preservation per unit time interval depends only on r/q and the interval length (Fig. 5.2.1.2).

Estimating completeness

This Section focuses on methods that seek an absolute, quantitative estimate of r, R, or P_P. In addition to these methods, there are a number of approaches based on the congruence between branching order and the order of stratigraphic first occurrences, and on the sum of lineage durations implied by a phylogenetic hypothesis but not actually preserved in the fossil record (Hitchin and Benton 1997). Such approaches are useful for providing a relative ranking of the quality of the fossil record of various higher taxa and environments, for cross-checking proposed evolutionary trees, and for focusing

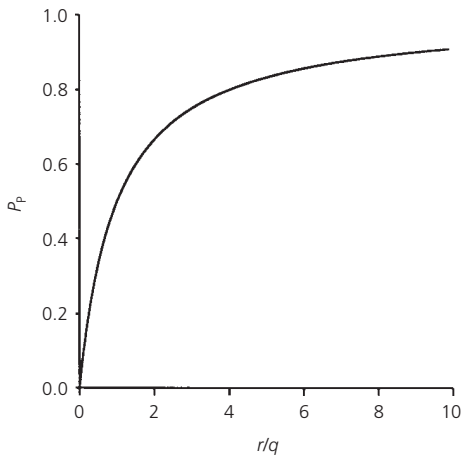

Fig. 5.2.1.1 Proportion of taxa preserved P_P as a function of the ratio of preservation rate r to extinction rate q. $P_P = r/(r+q)$ (Solow and Smith 1997). This relationship holds when the total span of time is very long relative to taxonomic duration.

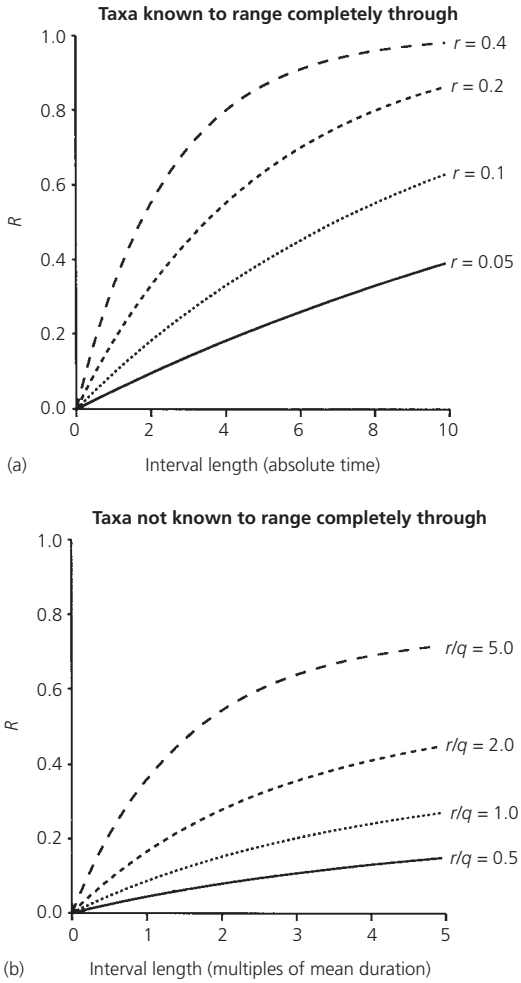

Fig. 5.2.1.2 Probability of preservation R per unit time interval. (a) If the taxon is known to range through the entire interval, then R is a function of the preservation rate r and the interval length t: $R = 1 - e^{-rt}$. (b) If the taxon is not known to span the entire interval, then R is a function of r, the interval length, and the origination and extinction rates (Foote 1997). Plotted here are the relationships when origination rate and extinction rate are equal. If interval length is expressed as a multiple of mean taxon duration, then R depends only on interval length and r/q. For example, R is the same if $q = 0.1$, the interval length is 20 myr (i.e. twice the mean duration), and $r = 0.2$, as it is if $q = 0.2$, the interval length is 10 myr, and $r = 0.4$.

attention on parts of the fossil record in particular need of study. It is difficult to use such approaches to measure absolute completeness, however, because poor congruence or large implied gaps may reflect error in phylogenetic estimates or the transformation of cladograms into evolutionary trees (including failure to recognize ancestor–descendant relationships), as well as palaeontological incompleteness. An important question for future work concerns the relative contributions of incompleteness and phylogenetic error to disagreements between stratigraphic data and genealogical hypotheses.

Estimates of completeness generally involve pooling taxa to gain a large statistical sample. This tacitly assumes taxonomic homogeneity of preservation rate, and, for some methods (Foote and Raup 1996; Foote 1997), homogeneity of extinction rate as well. When there is heterogeneity, the sample is biased toward the better-preserved groups, and the estimate of completeness is an average that is weighted more toward these groups. Temporal constancy of preservation rate is also a common assumption. Temporal variation will often be of little consequence, however, if it occurs on a time scale that is short relative to the average duration of taxa (which is not always the case; see below). How much heterogeneity is tolerable for a particular question can be explored by modelling (Foote and Raup 1996; Foote 1997).

Gaps and occurrences within stratigraphic ranges

Given a division of strata into discrete intervals and a tabulation of internal gaps (i.e. intervals in which a taxon must have existed, since it is found below and above, but was not preserved), R has been estimated as the ratio of the number of intervals in which a taxon is found to the total number of intervals in its range (Paul 1990). The logic of this approach is to consider whether a taxon is preserved during an interval in which, given our observation of its first and last occurrences, it has a chance to be preserved or not. This method gives an overestimate of preservation probability, however, since the intervals of first and last occurrence can never be gaps. An unbiased estimate is obtained by disregarding all intervals of first and last occurrence, which also involves disregarding all taxa with ranges of one or two intervals. For example, a taxon preserved in intervals 1, 3, and 5 yields an estimated R of 1/3, rather than 3/5. A taxon must have existed throughout an interval that falls between its intervals of first and last occurrence; thus, this estimate of R leads directly to an estimate of the preservation rate r (Fig. 5.2.1.2): $r = -\ln(1 - R)/t$.

The use of discrete time intervals is often required by the limited resolution of stratigraphic data. If data are available that more closely approach a continuous subdivision of time or stratigraphy, it may be desirable to use them to yield more precise estimates of preservation rates. In a continuous-time analogue of the method of tabulating internal gaps, the preservation rate r is estimated from the number of occurrences relative to the observed stratigraphic range (Solow and Smith 1997). Since the relationship between true duration and observed range depends on the preservation rate, extinction rate can also be estimated from the observed occurrence data (Solow and Smith 1997). This is of great importance, since differential preservability is one of the hindrances to comparing taxonomic rates of evolution among different groups. Given the estimates of extinction rate and preservation rate, it is possible to estimate the total proportion of taxa preserved (Solow and Smith 1997) (Fig. 5.2.1.1).

The analysis of gaps and occurrences is straightforward conceptually and in application. Although sampling error is high for single taxa, this can be greatly reduced by pooling taxa. These methods typically yield estimates of the completeness of the fossil record in local areas rather than globally. A limitation of these methods is that the detailed occurrence data they require are often unavailable.

Analysis of taxonomic range distributions

The requirement of detailed occurrence data can be onerous. An alternative approach, by taking advantage of the shape of stratigraphic range distributions to estimate R, requires data on first and last occurrences only. It is intuitively reasonable that, the poorer the fossil record, the greater the proportion of taxa confined to single stratigraphic intervals. Mathematical formalization of this intuition allows R to be estimated as the frequency ratio (*FreqRat*) f_2^2/f_1f_3, where f_1, f_2, and f_3 are the frequencies of taxa with observed stratigraphic ranges of one, two, and three intervals (Foote and Raup 1996). (A continuous-time analogue yields an estimate of r; Foote 1997.) This same formalization allows q to be estimated from the range-frequency distribution. Completeness P_P can thus be estimated as well. This approach works best when the original distribution of taxonomic durations is exponential (i.e. when extinction rate is constant). Like the analysis of gaps, it yields an estimate of local completeness. Since it uses less data, it has higher variance than estimates based on all occurrences. In cases where occurrence data are available, however, the two kinds of approaches have been found to yield compatible estimates of preservability (Foote 1997).

Proportion of living taxa with a fossil record

Estimates of the proportion of living taxa with a fossil record may be based on all known living taxa or just those known from a certain region; thus they can

provide completeness estimates at a range of geographical scales. A potential pitfall of this approach is that it may overestimate completeness when applied at higher taxonomic levels, even if preservation is homogeneous. This is because the chance of becoming fossilized depends in part on how long ago a taxon originated. There is some evidence that, for genera and higher taxa, the time-specific risk of extinction declines with taxonomic age. Taxa that happen to be alive today should therefore tend to be those that originated longer ago than average. Despite this probable bias, empirical comparison between the proportion of living families with a fossil record and the *FreqRat* for fossil genera has shown that these two measures are correlated.

Comparison between known diversity and estimated total diversity

Although the numbers are not firm and are changing daily, there are reasonable estimates of the number of described fossil taxa. One can estimate completeness P_P at a global scale by comparing this number to the estimated number of taxa that have ever lived. The latter figure is known with much less certainty, depending on estimates of taxonomic duration and on models of taxonomic diversity (including not just the pattern but also the magnitude). The estimate of total diversity is far more sensitive to the average taxonomic duration than to the details of the diversity model, and, happily, it is taxonomic duration that is easier to constrain empirically. A number of different estimates of this sort suggest that on the order of 1% of animal species within the skeletonized phyla are known (Foote 1996).

Corrections for incompleteness

Taxonomic durations

Observed ranges are generally shorter than true durations. Given an estimate of preservation probability from an analysis of gaps and occurrences, it is a fairly simple matter to infer a true original distribution from a distribution of observed ranges (Foote and Raup 1996). The true duration distribution can also be estimated directly (see above). Taxonomic longevity can thus be compared among groups with different preservational properties. In this way, it has been shown, for example, that the apparent difference in taxonomic longevity between mammals and bivalves is unlikely to be an artefact of the poorer preservation of mammals (Foote and Raup 1996).

Secular patterns of diversity, origination, and extinction

Observed diversity is generally lower than true diversity, but this may be acceptable provided that the observed pattern of diversity change is unbiased. The pattern is distorted, however, near the beginning and end of a stratigraphic succession. A principal reason for this edge effect is that the ability to infer the presence of a taxon by finding it below and above some stratum of interest diminishes toward the edges of the record (Pease 1985). Diversity drops artificially toward both edges, origination rate is artificially high toward the bottom edge, and extinction rate is artificially high toward the top edge. Another cause of edge effects is mass extinctions, prior to which last occurrences are artificially smeared backward. This problem has been treated by using detailed occurrence data to place confidence limits on the ends of taxon ranges (see Section 5.4.3). Edge effects have a number of quite distinct causes, but they can be modelled in a uniform way mathematically. Some explicit correction for edge effects should be possible, since the form of edge effects can be modelled, and preservation rates and true taxonomic durations can be estimated from incomplete data. This remains an important area for future work. A different problem concerns the relative diversities of groups with different preservational properties. Given adequate data, preservation rate and taxonomic duration can be estimated for each group separately, so that corrected diversity comparisons should be possible.

Phylogenetic analysis

Whether a sister-taxon relationship should be interpreted as a potential ancestor–descendant relationship depends partly on the completeness of the fossil record. Since ancestor–descendant pairs are more likely to be found as completeness increases, estimates of preservation rate and extinction rate allow us to predict the number of ancestor–descendant pairs that should be found. This can be used as a check on a proposed evolutionary tree. Whether the failure to observe a lineage in a particular stratum reflects a true or preservational absence is potentially important in the reconstruction of evolutionary trees; estimates of preservation probability are therefore essential (Foote 1996).

Discussion and prospects

Estimates of completeness generally increase with taxonomic rank, since progressively more species are included. Completeness tends to be lower at larger geographical scales, because the geological record consists of a geographical patchwork of fossiliferous and non-fossiliferous rock. Where the record exists, it is often rather complete for the well-skeletonized groups, with more than half of species preserved. Methods for estimating and correcting for incompleteness all have limi-

tations, but the estimates from different methods often agree, so one can have some confidence that these estimates are on the right track.

Future work will involve a more extensive tabulation of completeness and how it varies taxonomically, temporally, geographically, and environmentally. In addition, an especially important area is likely to involve a combination of modelling and empirical analysis to understand which approaches work best in particular circumstances. For example, the principles of sequence stratigraphy can be used to model the stratigraphic distribution of fossils (see Section 5.4.5). Such an exercise suggests that the *FreqRat* approach may sometimes be of limited use in single stratigraphic sections, not least because the time scale of variation in preservation probability is about the same as the time scale of species durations.

Another important area will involve the sensitivity of evolutionary patterns to incompleteness, with the goal of determining how strong a true pattern must be to be detected through an incomplete fossil record (or, how strong an observed pattern must be before one can be confident that it is not an artefact of incompleteness). For example, if one is interested in fluctuations in diversity, one can constrain, for a given level of diversity and preservation rate, how large a fluctuation must be to give some confidence that it is real. Along these same lines, it is also essential to explore how much preservation rate can vary before models and the corrections based on them begin to break down. A related task is to find measures of diversity, origination, and extinction that are relatively insensitive to incompleteness and heterogeneous preservation.

Finally, while agreement among various approaches is reassuring, discordances may also be illuminating. For example, if a phylogenetic estimate suggests few preserved ancestors while an estimate of preservation probability suggests that there should be many, this disagreement may suggest that ancestral taxa are less likely to be preserved, perhaps because their descendants rapidly displace them. Conversely, if hypothesized ancestors are more common than suggested by estimated preservation probability, this could imply that ancestral taxa are truly better preserved, perhaps because they are geographically widespread and thus more likely to give rise to daughter populations (Wagner and Erwin 1995).

Incompleteness does not thwart palaeontology. In many cases evolutionary patterns may not be seriously distorted, but, even when they are, our ability to estimate completeness quantitatively allows us to make explicit corrections, and thus to document and understand evolution in the fossil record.

References

Foote, M. (1996) On the probability of ancestors in the fossil record. *Paleobiology* **22**, 141–151.

Foote, M. (1997) Estimating taxonomic durations and preservation probability. *Paleobiology* **23**, 278–300.

Foote, M. and Raup, D.M. (1996) Fossil preservation and the stratigraphic ranges of taxa. *Paleobiology* **22**, 121–140.

Hitchin, R. and Benton, M.J. (1997) Congruence between parsimony and stratigraphy: comparisons of three indices. *Paleobiology* **23**, 20–32.

Paul, C.R.C. (1990) Completeness of the fossil record. In: D.E.G. Briggs and P.R. Crowther, eds. *Palaeobiology: a synthesis*, pp. 298–303. Blackwell Scientific Publications, Oxford.

Pease, C.M. (1985) Biases in the durations and diversities of fossil taxa. *Paleobiology* **11**, 272–292.

Solow, A.R. and Smith, W. (1997) On fossil preservation and the stratigraphic ranges of taxa. *Paleobiology* **23**, 271–277.

Wagner, P.J. and Erwin, D.H. (1995) Phylogenetic tests of speciation hypotheses. In: D.H. Erwin and R.L. Anstey, eds. *New approaches to studying speciation in the fossil record*, pp. 87–122. Columbia University Press, New York.

5.2.2 Analysis of Diversity

A.B. SMITH

Introduction

It is intuitively obvious that biological diversity has increased significantly since the beginning of the Phanerozoic. Important new plant and animal groups have appeared over the past 600 million years, and major new habitats have been created, invaded, and colonized. Accurate and reliable estimates of species diversity over geological time are clearly needed if we are to improve our understanding of the processes that have governed diversity. Yet such estimates remain extraordinarily difficult to obtain. Although the fossil record provides direct evidence for how biodiversity has changed over time, it cannot necessarily be taken at face value because of the bewilderingly large number of biases that act upon it. A proper appreciation of these biases is only now beginning to emerge.

Measures of diversity

Diversity can be measured in a number of different ways, each capturing a different, but related, aspect. Species diversity is a direct estimate of the numbers of biological species existing at any time. Taxonomic diver-

sity measures the numbers of supra-specific taxa as a proxy for species diversity. Morphological diversity addresses the variety of body forms that have evolved, while genetic diversity, though not applicable to fossils, measures the variation that exists in genomic structure amongst taxa. Ecological diversity estimates the amount of adaptive space occupied by taxa.

Diversity can be assessed at different scales, from detailed studies of changes occurring in a single section, through to global studies. Total diversity is a combination of the degree of packing of species within individual communities or localities (alpha diversity), the differentiation created by relative habitat and community heterogeneity within a single region (beta diversity), and the diversity created by regional differentiation (gamma diversity). Accurate assessment becomes progressively more difficult as the scale increases because of the assumptions that must be added when calculating diversity.

There are two principal components to diversity: richness and disparity. Richness refers to the number of kinds that can be recognized while disparity (see Section 5.1.3) refers to the degree of differentiation amongst kinds. Although the two components are measured independently, the correct interpretation of disparity is dependent upon the accuracy of our estimate of species richness. An increase or decrease in species richness may cause disparity to change, but if this reflects sampling problems in the fossil record rather than true changes in biodiversity, then our interpretation of disparity may be ill-founded.

Species diversity

Counting the number of species coexisting at any one time is clearly the simplest and most direct measure of diversity. Yet obtaining accurate estimates from the fossil record is difficult. Although the number of species described for each geological period can be estimated, the relationship between observed and true diversity is distorted by a large number of confounding factors.

Only a small proportion of organisms ever enter the fossil record. Animals lacking a durable skeleton are preserved only under exceptional conditions, leaving those with robust skeletons and high fossilization potential to dominate the record. This is no serious problem as long as the ratio of skeletalized to non- or weakly-skeletalized organisms has remained more or less constant, which may not necessarily be true. One possible source of error arises because, in many marine invertebrate groups, skeletons have become progressively more robust over time. Thus the rigid thick-shelled skeleton of a Tertiary sand-dollar (echinoid) is much more robust than the skeleton of any of its Palaeozoic antecedents and the fossilization potential of echinoids in general has improved over time.

Differences in skeletal structure and biomineralogy strongly influence preservation potential and distort the fossil record. In molluscs, for example, aragonitic-shelled taxa are more readily lost from the fossil record than calcitic-shelled taxa. Time intervals or geographical regions where conditions favouring aragonitic preservation are more infrequently encountered will appear to have a lower diversity. Furthermore, taxa with more durable skeletons will appear to be widespread and long-lived in comparison to their less robust relatives (Koch 1998).

Preservational biases act in a number of ways, most of which tend to decrease the quality of the fossil record further back in time (Table 5.2.2.1; see Signor 1990). For example, older geological intervals have smaller outcrop area and increased diagenetic and tectonic overprinting, which tend to decrease the chances of their fossil biota surviving and being discovered. The quality of the fossil record is particularly susceptible to changes in the sedimentary depositional framework. Sequence stratigraphic modelling suggests that depositional cycles driven by sea-level change play a major role in driving the fossil record by altering sedimentation patterns and water depth on a regional basis (Holland 1995; Brett 1998). Such changes alter the distribution of facies and species distributions, directly influencing perceived diversity in the fossil record. For many marine macroinvertebrates diversity is highest in shallow open-shelf environments (due to habitat heterogeneity) and

Table 5.2.2.1 Major factors known or suspected to correlate with species richness.

1 Surface outcrop area	Diversity correlates with amount of rock cropping out and available for study
2 Palaeontological interest	Diversity may reflect the numbers of palaeontologists actively interested in collecting and monographing the biota
3 Palaeocontinental distribution	Position of well-studied continents (North America, western Europe) has shifted over geological time from tropical to temperate. If low-latitude faunas are more diverse then this may affect patterns
4 Higher order sea-level trends	Long-term sea-level trends control the predominance of either deep shelf or broad onshore platform facies preserved regionally.
5 Geological age	Younger rocks are less altered and may offer better preservation

decreases towards outer shelf and basinal settings. Platform flooding events shift these higher-diversity onshore environments far on to cratons where they subsequently become highly susceptible to erosion and loss from the fossil record during regressive system tracts (Fig. 5.2.2.1). Major platform flooding events should therefore create an apparent drop in marine benthic diversity caused by under-representation or removal of onshore facies during high stand and regressive system tracts. Furthermore, because most species in the fossil record are rare, under-representation of onshore shelf facies will exacerbate the perceived drop in diversity. This pattern is clearly evident in the Cretaceous, where the three major platform flooding events in western Europe (Aptian, end-Cenomanian, and end-Maastrichtian) coincide with 'extinction' peaks in marine macroinvertebrates. It seems likely that major global changes in sea level and concomitant depositional architecture are at least partially responsible for creating the apparent rise and fall of diversity over time intervals of 1–30 million years.

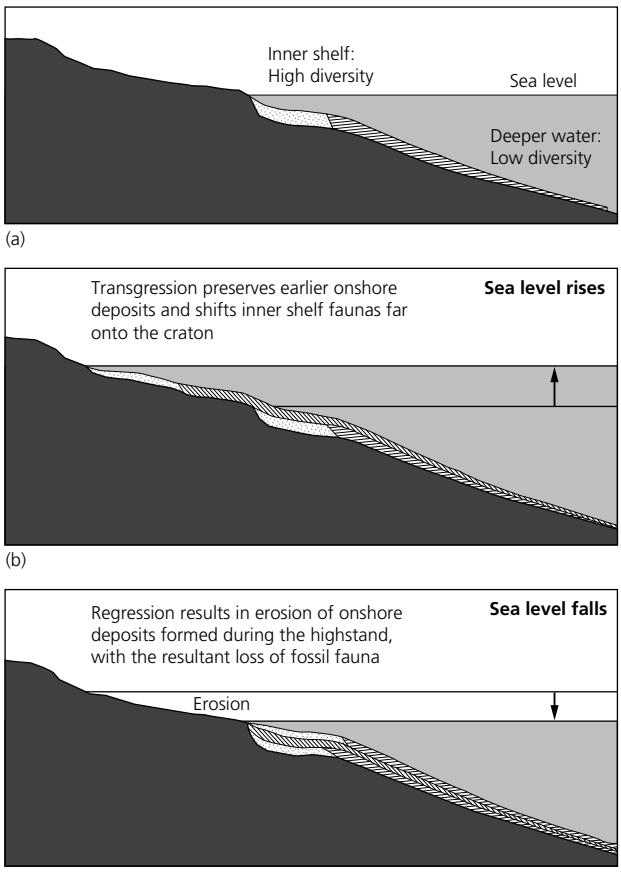
Inner shelf:
High diversity
Sea level
Deeper water:
Low diversity
(a)
Transgression preserves earlier onshore deposits and shifts inner shelf faunas far onto the craton
Sea level rises
(b)
Regression results in erosion of onshore deposits formed during the highstand, with the resultant loss of fossil fauna
Sea level falls
Erosion
(c)

Fig. 5.2.2.1 Model showing how changes in sea level could artificially create variation in species diversity in the fossil record.

Raw species counts therefore generally end up tracking the outcrop area of fossiliferous strata rather than biological diversity. For marine invertebrates there is a remarkably close correspondence between apparent species diversity and preserved rock volume (Signor 1990).

Taxonomic diversity

Because species-level counts are so susceptible to preservational biases, diversity analysis is commonly carried out at higher taxonomic levels (genera, families, orders). Moving to more inclusive taxonomic units should reduce sampling problems since, on average, higher taxa contain more species and only one species need be discovered for the taxon to be registered as present. Usually ranges of taxa are interpolated between first and last records, irrespective of whether they have actually been discovered in any intermediate horizons. Although this procedure helps dampen the distorting effects of preservational biases, it introduces additional problems:

1 Because taxonomic rank has been assigned by taxonomists for a variety of different reasons, there is no fixed relationship between numbers of species and taxonomic rank. Indeed, the modal number of taxa within any higher taxonomic level is 1 (Signor 1990), and the increase in species evident in higher taxonomic levels is generated solely by increase in variance. In other words, higher taxa comprise a more variable number of species than do lower taxa and consequently appear, on average, to be more diverse.

2 Diversity estimates make the assumption that average species composition of higher taxa has remained stable over time. This is demonstrably false, since taxonomic practice has led to a distinct bias in the species richness of higher taxa over geological time. Early Palaeozoic and early Mesozoic families contain fewer species than do later Palaeozoic and later Mesozoic and Tertiary families, respectively. Although this might conceivably have some biological basis, it is more likely to reflect the way in which taxonomists have bestowed high rank to early taxa that do not fit comfortably into modern crown-group diagnoses.

3 Patterns of Phanerozoic diversity calculated at high and low taxonomic levels disagree. This arises from the interplay of two factors: preservational biases acting on the quality of the fossil record, and taxonomic biases affecting the species composition of higher taxa. The more inclusive the taxon, the less reliable it is as an indicator of species diversity (Signor 1990). On the other hand, the lower the taxonomic rank, the more monospecific groups it contains (Smith 1994) and the more likely it is that the pattern is influenced by the quality of the fossil record and sampling artefacts. A common compromise is to work at the family level. Yet plots of

species, genus, and familial diversity all follow more or less the same trajectory over time, so it would appear that many of the biases known to afflict species-level data are still present in family-level data.

4 Much of the existing database is composed of non-monophyletic taxa. This makes no difference to estimates of standing diversity, but it can affect extinction and origination estimates (Smith 1994). Whereas the disappearance of a monophyletic taxon plausibly represents extinction of that lineage, the disappearance of a non-monophyletic taxon can arise because a taxonomist has arbitrarily chosen to impose a name change (pseudoextinction). Gaps in the fossil record created by sequence architecture often act as convenient breakpoints at which to split a single lineage into a derived monophyletic clade and an earlier paraphyletic grade. Such pseudoextinctions are predicted to cluster at major system boundaries.

Estimating changes in diversity from successively more inclusive higher taxa progressively dampens extinction signal (many species within a taxon may go extinct, but only a single species need persist for the higher taxon to survive). Conversely, moving to lower taxonomic levels increases the proportion of taxa based on a single species, whose distributions are likely to be strongly influenced by the quality of the fossil record. Furthermore, taxonomic data that are dominated by non-monophyletic taxa will do little more than track the quality of the fossil record. A more accurate picture of diversification and extinction in the fossil record is obtained by using only monophyletic taxa.

Morphological diversity

Morphological diversity (disparity: see Section 5.1.3) can be approached either quantitatively, for example using landmark techniques to measure changes in shape (see Section 5.1.2), or in a semiquantitative way by defining discrete characters. The former is more objective as long as landmarks are based on homologous points. However, it is applicable only to conserved structures and cannot address morphological diversity in any meaningful way across diverse groups. The latter is more generally applicable but requires subjective recognition of discrete character state changes that in some way encapsulate the differences seen amongst taxa.

There are also two complementary methodological approaches. One approach is to ask how much morphological separation exists amongst the taxa being compared, and how this has changed by comparing different time slices. The other is to estimate how much evolutionary change (including reversals and parallelisms) has taken place by a specific time after initial divergence. The former is a phenetic approach, the latter requires a phylogeny.

Genetic diversity

Although genetic similarity (e.g. measured by DNA–DNA hybridization or gene sequence comparison) is only really obtainable from extant species, it can provide insight into historical patterns of change. For example, analysis of gene sequences in insects demonstrates that there was a 20-fold increase in the rate of fixed point mutation in the stem group of dipterans. By calibrating the cladogram against the fossil record, this short burst of genomic diversification can be shown to have occurred between 250 and 210 million years ago (Friedrich and Tautz 1997).

Correspondence of morphological, genetic, and taxic diversity

How do different measures of diversity correspond? Little systematic investigation of this subject has been carried out. The only broad study of morphological and genetic divergence (Ormland 1997) found that rates of morphological and molecular evolution are surprisingly well correlated, with statistically significant positive correlation between molecular and morphological branch lengths in seven out of eight case studies. This suggests that genetic and morphological diversity provide broadly comparable estimates.

The correspondence between taxic and morphological diversity is more problematic. Most studies point to a marked decoupling between morphological and taxic diversity during the early history of major higher taxa (see Section 5.1.3).

Improving the accuracy of diversity estimates

All estimates of diversity based on raw counts are distorted to a greater or lesser extent by taxonomic, sampling, and preservational biases (Koch 1998). These distortions need to be identified and then compensated for if we are to improve the accuracy of our estimates. To do this we need access to other data, namely phylogenetic hypotheses, sequence stratigraphic modelling, or relative abundance data.

Incorporating information from phylogeny

Where well-corroborated phylogenetic hypotheses exist, these can be used to compensate for sampling biases and gaps in the fossil record. Sister taxa by definition must have the same time of origin. Therefore the earliest appearance of either taxon in the fossil record immediately establishes the minimal age of origin of the other. Utilizing phylogenetic information can in some cases lead to considerable extensions to the known taxonomic ranges. These inferred portions of a taxon's range for

which there is no direct evidence, but which are made apparent when phylogenies are combined with stratigraphy, are termed ghost lineages. They form an important source of information about diversity that cannot be recovered from a direct reading of the fossil record.

By calibrating a phylogenetic hypothesis against the known stratigraphic ranges of taxa, we can recognize intervals of time when taxa must have existed but have yet to be discovered. Phylogenetic hypotheses thus allow range extensions to be made outside the first and last occurrence points, whereas range interpolation using higher taxa fills in gaps only between the first and last occurrences. This method is, however, dependent upon the correctness of the phylogenetic hypothesis.

Incorporating field information

Sequence stratigraphic modelling of sedimentary regimes is revolutionizing our understanding of the factors controlling fossil distribution on local and regional scales. Relative sea-level changes influence apparent species diversity at system bases and major flooding surfaces through altering the prevailing depositional regime. Furthermore, first and last occurrences tend to cluster around sequence boundaries (Holland 1995). Integrating diversity and abundance data with sequence stratigraphic models through field-based studies will clearly lead to a better appreciation of taphonomic and sampling biases and thus lead to refined estimates of biodiversity patterns through time.

Utilizing abundance and distributional data

Before accepting variation in species diversity as biologically meaningful, it is crucial that differences in sampling intensity are factored out (Koch 1998). Is a difference in recorded diversity between two localities or horizons simply the result of differences in sampling, or is there a genuine biological signal? To resolve this question, information on sampling intensity is needed, either in the form of numbers of individuals or numbers of fossil localities.

Ideally, knowledge of the absolute numbers of specimens collected is needed to compensate for sampling biases, but approximations can be made. For example, a plot of the number of marine invertebrate genera recorded from each stage of the Ordovician suggests that there was a marked drop in diversity in the Llanvirn. However, this takes no account of the varying time spans represented by individual stages, nor the number of fossiliferous localities in each. A more accurate picture emerges when the total number of records in each stage is used as an estimate of sampling intensity, and the data from each period reduced to a standard size by rarefaction. When this is done, the apparent extinction and dip in diversity in the Llanvirn turns out to be a sampling artefact (Fig. 5.2.2.2).

Using only information on the occurrence, but not the absolute numbers of fossils, within predetermined time intervals, it is possible to derive an estimate of the completeness of the fossil record (Foote and Raup 1996; Foote 1997). The method uses the gaps within

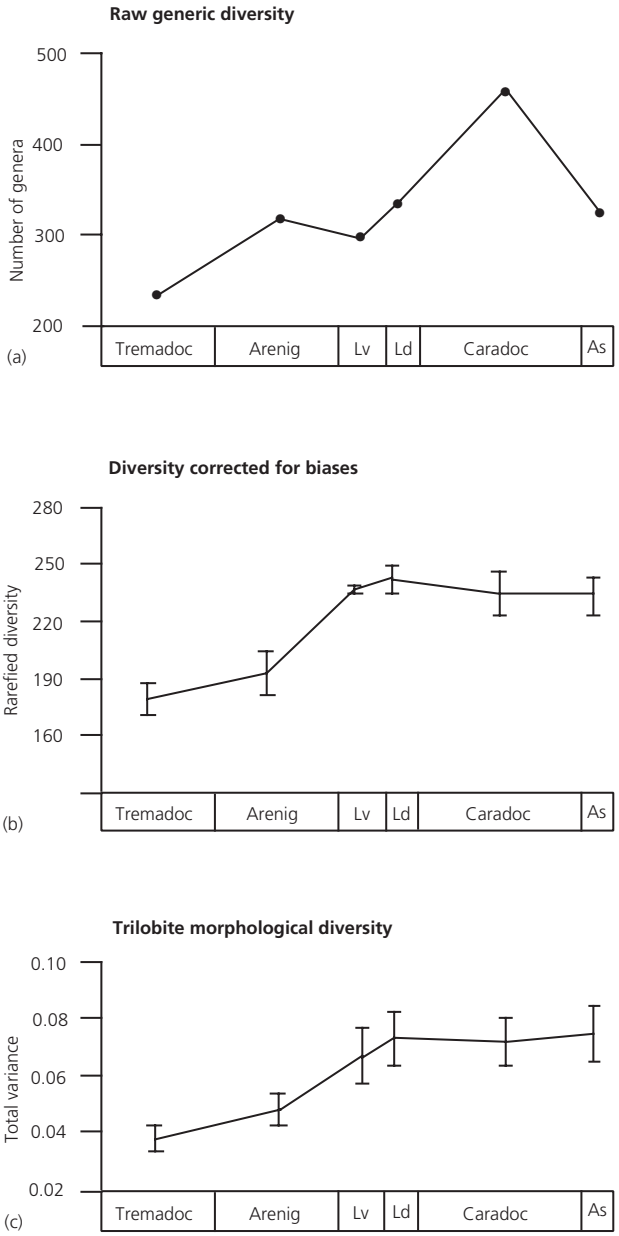

Fig. 5.2.2.2 Estimates of genus-level diversity for Ordovician marine invertebrates (trilobites, brachiopods, bivalves, gastropods, and monoplacophorans). (a) All taxa, with no compensation made for sampling bias. (b) Diversity estimates after rarefaction to compensate for unequal sampling. (c) Trilobite morphological diversity over the same time interval. (From Miller and Foote 1996.)

individual taxonomic ranges to estimate how much of the taxon's range is missing before and after its first and last appearance. The observed range of the total estimated duration summed over all taxa provides a measure of the quality of the fossil record. This approach is surprisingly resilient to variation in preservational potential. However, it is important to remember that only local and/or regional completeness is estimated, i.e. it provides an indication of how well sampled species are in known outcrops, but not how much of the global fauna is represented by the fauna of those outcrops.

Summary

Accurate estimates of species diversity through the Phanerozoic are needed to understand how evolution has proceeded. Counting species or higher taxa provides a useful first approximation, but this approach has fundamental weaknesses because of biases in the fossil record and biases in taxonomic practice. Improved estimates can be achieved through the application of more sophisticated statistical approaches to compensate for sampling irregularities, and through the incorporation of phylogenetic information and a knowledge of the sequence stratigraphic framework.

References

Brett, C.E. (1998) Sequence stratigraphy, paleoecology, and evolution: biotic clues and responses to sea-level fluctuations. *Palaios* **13**, 241–262.

Foote, M. (1997) Estimating taxonomic durations and preservation probability. *Paleobiology* **23**, 278–300.

Foote, M. and Raup, D.M. (1996) Fossil preservation and the stratigraphic ranges of taxa. *Paleobiology* **22**, 121–140.

Friedrich, M. and Tautz, D. (1997) An episodic change of rDNA nucleotide substitution rate has occurred during the emergence of the insect order Diptera. *Molecular Biology and Evolution* **14**, 644–653.

Holland, S.M. (1995) The stratigraphic distribution of fossils. *Paleobiology* **21**, 92–109.

Koch, C. (1998) 'Taxonomic barriers' and other distortions within the fossil record. In: S.K. Donovan and C.R.C. Paul, eds. *The adequacy of the fossil record*, pp. 189–206. Wiley, Chichester.

Miller, A.I. and Foote, M. (1996) Calibrating the Ordovician radiation of marine life: implications for Phanerozoic diversity trends. *Paleobiology* **22**, 304–309.

Ormland, K.E. (1997) Correlated rates of molecular and morphological evolution. *Evolution* **51**, 1381–1393.

Signor, P.W. (1990) The geological history of diversity. *Annual Review of Ecology and Systematics* **21**, 509–539.

Smith, A.B. (1994) *Systematics and the fossil record: discovering evolutionary patterns*. Blackwell Scientific Publications, Oxford.

5.3 Reconstructing Phylogeny

5.3.1 Phylogenetic Analysis

M. WILKINSON

Introduction

Within lineages, including our own species, all individuals have genealogical relationships that are the product of their reproductive history. The most direct genealogical relationship within lineages is that between a parent (ancestor) and offspring (descendant). Individuals that are not related so directly share more indirect relationships (e.g. siblings, cousins, and so on) by virtue of their shared common parentage. Phylogenetic relationships are the genealogical relationships that exist between distinct lineages. They are the product of both reproduction and evolutionary divergence, and are often evocatively conceptualized as forming one great phylogeny, the Tree of Life. Phylogenetic analysis is primarily concerned with reconstructing cladistic relationships: the branching pattern connecting lineages in parts of the Tree of Life. Trees or cladograms represent hypothesized branching patterns (Fig. 5.3.1.1) and sometimes include additional information, such as an absolute time scale or amounts of change associated with individual branches. In addition to their intrinsic interest, phylogenies are used as historical frameworks for the study of diverse evolutionary phenomena, from adaptation to zoogeography.

Although phylogeny can be thought of as genealogy writ large, there are important differences between genealogical relationships within and between lineages.

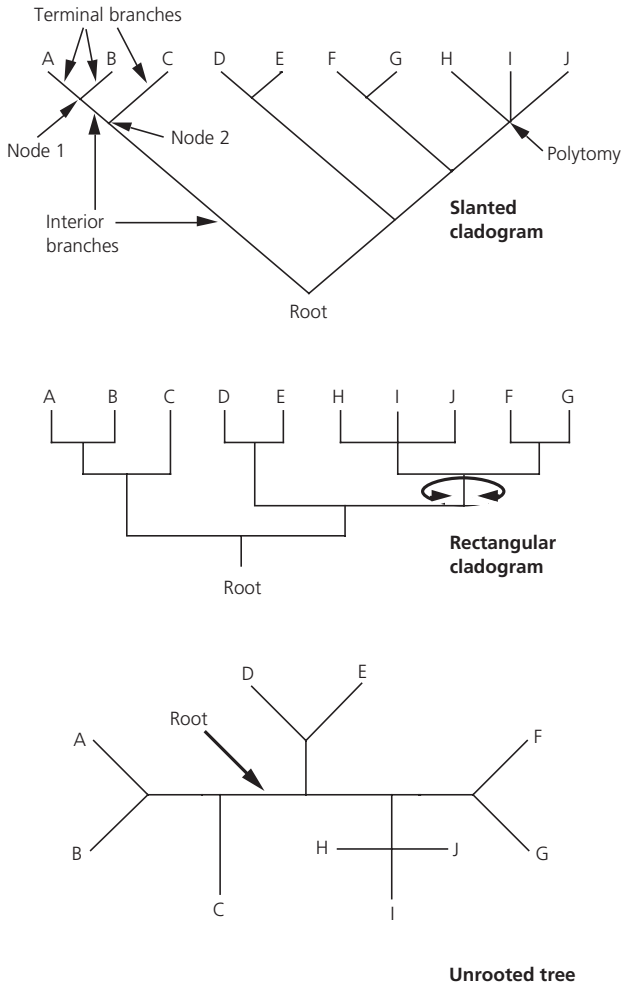

Fig. 5.3.1.1 Trees of phylogenetic relationships. Each tree is composed of: terminal branches leading to the taxa A–J under consideration; internal branches that represent hypothetical ancestral taxa; and nodes at which branches are joined together and which represent the hypothesized splitting of lineages. The first two trees are rooted cladograms that differ only stylistically, and which include the same cladistic relationships. Each node identifies a clade and a sister-group relationship. For example, node 1 identifies the clade comprising taxa A and B and the sister-group relationship between A and B. Similarly, the group F–J is a clade and it is composed of two less inclusive clades F–G and H–J that are sister-groups to each other. In the rectangular cladogram the relative positions of these sister-groups have been rotated, but this does not affect the relationships that are represented. Groups can be rotated freely about the nodes that unite them. The cladograms are incompletely resolved because they contain a polytomy. Polytomies can be interpreted as multiple branching, but are more usually interpreted as uncertainty over the branching sequence and cladistic relationships. Cladograms do not have an absolute time scale (although a time scale can be incorporated by mapping the cladogram against stratigraphy). However, they do have a time dimension that is given by the root. The order in which nodes are encountered from the root to any terminal branch corresponds to the hypothesized temporal order of lineage splitting. For example, node 1 represents the splitting of the last common ancestor of A and B and this occurred after the splitting of the last common ancestor of A, B, and C (node 2). Such comparisons cannot be extended across different parts of the cladogram. For example, the tree provides no information on the relative recency of node 1 and the polytomous node uniting H–J. Numerical phylogenetic analyses typically produce unrooted trees. Unrooted trees, like the third tree shown here, are consistent with various cladistic relationships in rooted trees but do not themselves specify clades or sister-groups.

Firstly, sexual reproduction *within* lineages produces a complex reticulate network of genetic relationships. Much of the phylogeny of life, on the other hand, which reflects relationships *between* lineages, is tree-like rather than reticulate (although hybridization, endosymbiosis, and horizontal transfer of genes may lead to partial or complete anastomoses between lineages). Secondly, from a genetic perspective your parents are as closely related to you as they are to their own parents. Organisms share the same proportion of genes with their parents as they do with their offspring (50% in sexually reproducing forms and 100% in clonal reproduction). In contrast, closeness of cladistic relationships is defined in terms of the branching pattern of phylogeny; it reflects only relative recency of common ancestry, and is always a comparative concept. In cladistic terms two or more taxa are more closely related to each other than they are to some other taxa if they share a common ancestor that is not also a common ancestor of any of the other taxa. Consequently, closeness of cladistic relationships may or may not coincide with overall genetic similarity.

For much of the twentieth century, phylogenetic analysis has been particularly associated with palaeobiology. This reflects a long-standing focus on the reconstruction of ancestor–descendant sequences of lineages, for which a fossil record is indispensable. Where the fossil record is particularly complete (e.g. for planktic Foraminifera), the reconstruction of ancestor–descendant sequences, by means such as stratophenetics (Gingerich 1979), remains extremely useful. However, for the majority of groups the incompleteness of their fossil record precludes the search for direct relationships of ancestry and descent. Modern methods of phylogenetic analysis have been developed for inferring more indirect relationships in the absence of any record of actual ancestors. In particular, these methods aim to recover clades (groups that are monophyletic in the sense of comprising taxa that are more closely related to each other than they are to any taxa not included in the group) and sister-groups (clades that are each other's closest relatives and thus together comprise a more inclusive clade).

Evidence of relationships

Phylogenetic analysis is an historical science that attempts to infer patterns of relationships that are the product of evolutionary events (splitting of lineages). Typically these events occurred in the distant past and are not directly observable. What then provides evidence of these long-past events and the pattern of relationships they produce? The evidence comes in the form of heritable similarities and differences in the characteristics of taxa (any lineage or monophyletic group of lineages). Taxa display a multitude of similarities and differences at all levels of organization, and phylogeneticists typically represent this underlying variation as a series of discrete characters (each representing a separate basis for comparison). In turn, each character comprises a number of discrete character states (categories into which the variations fall or can be partitioned). Characters can be formulated from any aspect of the genotype or phenotype, but in palaeobiology they are limited by preservation potential and are almost always morphological. The simplest characters have just two character states, e.g. the absence or presence of hair. Multistate characters have three or more character states, e.g. the number of temporal fenestrae in amniotes (none, one, or two). Assembling a dataset summarizing the distributions of character states across the taxa under consideration, for as many characters as is practical, is an essential step in phylogenetic analysis because it determines the results of any numerical analyses. Despite its importance, the ways in which morphological characters are formulated is an understudied aspect of phylogenetic analysis that leaves much room for subjectivity and disagreement (Wilkinson 1995).

Differences between the character states of taxa are the product of evolutionary changes within ancestral lineages. These changes have a direction or polarity, reflected in the difference between relatively ancestral (plesiomorphic) and derived (apomorphic) character states. In contrast, similarities within character states can be explained in two ways, homology and homoplasy, that differ in the amount of change between character states. Two taxa could inherit the same character state from their last common ancestral lineage, in which case the similarity is homologous. The distribution of homologous character states of a binary character can be explained by: (1) an hypothesis of relationships, specifically a tree in which the taxa with the derived character state form a clade; and (2) an hypothesis of a single change from the ancestral to the derived state in the last common ancestor of the clade (e.g. Fig. 5.3.1.2, Tree A). Thus hypotheses of homology and of transformation are crucial to the inference of cladistic relationships from observed similarities. The alternative explanation of similarities is as the result of homoplasy:

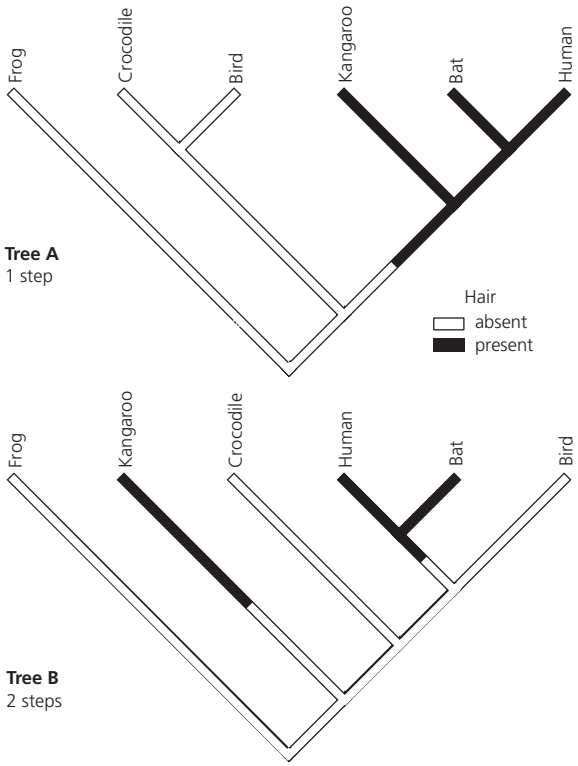

Fig. 5.3.1.2 Parsimonious character optimization. Trees A and B show two alternative sets of cladistic relationships for a selection of tetrapods and the fit of a single character (the presence or absence of hair) to these trees. In Tree A, the three mammal taxa are a clade, and the presence of hair in the mammals and its absence in the non-mammals can be explained with a single origin (step) of hair in the last common ancestor of the mammals. In contrast, Tree B requires a minimum of two steps to explain the observed distribution of the character states, with separate origins of hair in the line leading to the kangaroo and in the last common ancestor of the human and the bat. More complex character histories (with multiple origins and repeated losses) could be considered but parsimonious character optimization minimizes the number of steps required to explain the observed distributions of the character states. Both homoplasy and missing data can lead to alternative equally parsimonious character optimizations on a single tree. Most importantly, trees can differ in the minimum number of steps required to explain the observed distributions of the character states, and this provides a basis for choosing between alternative trees.

multiple changes between character states (convergences, parallelisms, or evolutionary reversals). Unlike homology, hypotheses of homoplasy can be formulated to fit any tree. In addition, homoplasy can provide potentially misleading evidence of cladistic relationships if mistakenly interpreted as homology. This aspect of homoplasy presents the greatest challenge to the accurate inference of cladistic relationships.

Phylogenetic analysis is built upon a preference for

homology over homoplasy as an explanation for similarity. Indeed, similarities provide evidence of cladistic relationships to the extent that homology provides a better explanation of similarity than does homoplasy. However, homoplasy is known to be widespread (and therefore a problem) because almost all published cladistic datasets include characters that provide conflicting evidence of cladistic relationships. How do we proceed in the face of such conflicting evidence? Classically, conflicts were resolved, as far as possible, by considering the conflicting characters with the expectation that homoplastic similarities will be more superficial than homologous similarities. For example, birds and many insects have wings but this resemblance is structurally and developmentally superficial. In contrast, numerous detailed similarities exist between insects and other arthropods and between birds and other vertebrates. Both the more detailed nature of these similarities individually, and their greater number collectively, provide overwhelming evidence that birds and insects belong to widely separated parts of the Tree of Life. Such considerations allow the possession of wings to be identified as a homoplastic similarity between insects and birds. Modern phylogenetic analyses use computerized numerical techniques to weigh the evidence for alternative cladistic relationships and thereby emphasize the agreement or congruence between the independent evidence provided by multiple characters.

Parsimony analysis

Molecular sequence data can be analysed with a wide range of techniques (see Section 5.3.4), but parsimony analysis is the main numerical technique used to infer cladistic relationships from morphological character data. Parsimony analysis is a simple method but there are numerous potential complications (Swofford and Begle 1993). It is based upon the idea of parsimonious character optimization. Given any tree and any character, the distribution of the character states across the taxa under consideration can be explained by mapping hypothesized changes in character states (steps) on to particular branches in the tree (Fig. 5.3.1.2). Under parsimonious character optimization, the number of steps is minimized and the fit of the character to the tree is maximized. The number of steps required to account for the observed distribution of the states of a character can differ on different trees (Fig. 5.3.1.2). The better the fit, the more similarity that can be explained as homology. Parsimonious optimizations can be determined independently for each of a set of characters on any tree. Typically some characters will fit a tree well (require few steps) while others will fit it badly (require many steps). In the simplest form of parsimony analysis, the total number of steps required to explain the observed distributions of all the states of all of the characters, termed tree length, is used to discriminate between alternative trees. Preferred hypotheses are those that minimize 'tree length' (Fig. 5.3.1.3) and thereby maximize the amount of similarity that can be explained by homology.

In the simplest parsimony analyses, each step contributes an equal cost to tree length, irrespective of the type of change represented. This corresponds to equal weighting of the evidence provided by the potentially diverse characters. Parsimony analysis can also be performed with unequal weighting, such that different changes contribute different increases in tree length. In such cases, tree lengths are a weighted sum of the steps required and the shortest tree does not necessarily maximize the amount of similarity that can be explained as homology. Character weighting is a vexed issue upon which opinions are divided. In practice most workers use equal weighting and some view differential character weighting as unjustifiable. However, several promising methods of character weighting have been developed and these deserve further study (Swofford *et al.* 1996).

When the number of taxa included in the study is sufficiently small, it is possible to examine all possible trees, either explicitly or implicitly, and identify all the most parsimonious trees (MPTs). However, the number of possible trees increases exponentially with the number of taxa. This precludes such exact searches in many cases and necessitates the use of heuristic search strategies. These can evaluate only a proportion of the possible trees, and therefore do not guarantee finding MPTs.

Outgroups and rooting

The alternative trees of Fig. 5.3.1.3 are rooted so that the frog is the sister-taxon of all amniotes. Rooted trees comprise sets of clades and are the focus of phylogenetic analysis. However, parsimony analysis typically is performed on unrooted trees in the absence of any consideration of character polarity. Unrooted trees are then converted to rooted trees.

One approach to rooting is to infer the ancestral character state of each character separately, include a hypothetical ancestral taxon with these character states in the analysis, and root the tree at the point where the hypothetical ancestor joins the other taxa. A number of criteria have been proposed for determining which character states are ancestral and which are derived, the most important of which is 'outgroup comparison' (Maddison *et al.* 1984). Characters which vary within the group under study (the ingroup) are polarized on the basis of those character states that are present in other taxa (outgroups). The outgroup, in its broadest sense, includes all taxa that are not part of the ingroup (typically taxa that

		CHARACTERS						
		1	2	3	4	5	6	
		amnion	hair	lactation	placenta	antorbital fenestra	wings	
TAXA	Frog	–	–	–	–	–	–	
	Bird	+	–	–	–	+	+	
	Crocodile	+	–	–	–	+	–	
	Kangaroo	+	+	+	–	–	–	
	Bat	+	+	+	+	–	+	
	Human	+	+	+	+	–	–	TREE LENGTH
FIT	Tree A	1	1	1	1	1	2	7
	Tree B	1	2	2	2	2	1	10

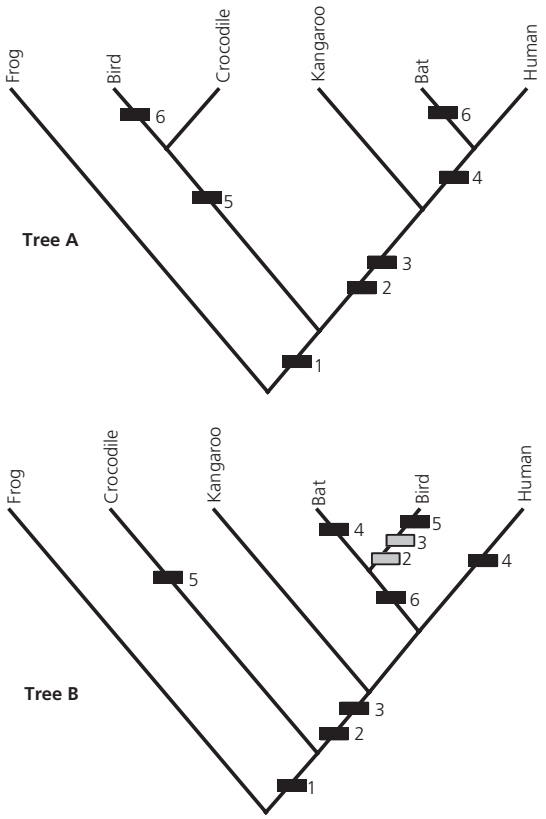

Fig. 5.3.1.3 A simple example of parsimony analysis. The data matrix summarizes the distributions of the character states, present (+) and absent (–), of six binary characters across six tetrapod taxa. The characters can be optimized on to any tree and tree length determined as the sum of the number of steps required to explain the observed distributions of character states. Two of the 945 possible rooted trees are shown here. Of the two, Tree A is the more parsimonious. In fact Tree A is the single MPT for the data. Characters 1–5 fit Tree A perfectly, so that all similarity in these characters is explained by common ancestry and homology, and only character 6 requires homoplasy on this tree. Character 6 conflicts with characters 2–5 in that they provide evidence for contradictory phylogenetic relationships. On Tree B, character 6 fits perfectly but the conflicting characters 2–5 all require homoplasy and contribute to the greater length of this tree. Changes from absence to presence are indicated by solid boxes and from presence to absence (evolutionary reversals) by grey boxes.

are thought to be closely related to the ingroup are used). In the simplest case, if just one of two ingroup character states is found also amongst the outgroups, then it is considered ancestral. This polarity assessment is maximally parsimonious. The alternative, in which the unique ingroup condition is considered ancestral (and thus assigned to the root of the ingroup tree), requires homoplasy to explain the similarity between the outgroup and ingroup. Polarity decisions may also be based on stratigraphic precedence; the oldest known character state is considered ancestral. Erroneous polarity assessments can arise because of homoplasy or incompleteness of the fossil record.

A simpler and more common approach to rooting is to include in the analysis one or more representative outgroup taxa from the rest of the Tree of Life. The root of a tree for a particular ingroup represents an hypothesis of the place at which the ingroup tree is joined to the rest of the Tree of Life. Unrooted trees, including both outgroup and ingroup taxa, can thus be rooted where the ingroup taxa join the outgroups. Trees are rooted without any specific consideration of character polarity. The location of steps is determined by the parsimonious character optimization on the unrooted MPT, and the direction of change reflects the rooting.

Multiple trees

Parsimony analysis does not always yield a single MPT. Usually this is because there are equally parsimonious interpretations of which similarities are homoplastic and which homologous. In addition, inclusion of fossils that are too incomplete to limit their inferred phylogenetic positions can lead to a multitude of equally parsimonious trees. Faced with multiple MPTs it may be possible to choose among them using some secondary criteria. Proposed criteria include the distribution of homoplasy, and fit to stratigraphy. However, where a single pre-

ferred tree cannot be identified, a consensus tree may be used to provide a conservative hypothesis of phylogeny based on agreement among the MPTs. The simplest consensus tree includes only those clades that are found in all the MPTs, and which are therefore unambiguously supported under all the most parsimonious interpretations. Polytomies in such consensus trees represent areas of disagreement among the MPTs on which judgement is reserved. Clade-based consensus trees may be very poorly resolved when multiple trees result from the instability of particular taxa. Under these circumstances consensus methods that identify and prune unstable taxa provide a useful alternative approach (Wilkinson and Benton 1996).

Assessing phylogenetic hypotheses and data

Too many phylogenetic studies end with the discovery of an MPT, or a consensus of MPTs, and the associated reconstructions of character state changes. However, it is important to consider also the 'robustness' of inferred cladistic relationships. Several measures of the degree of support for particular clades are available. One approach is to compare the relationships in MPTs with those in slightly less parsimonious trees. Some clades found in all the MPTs may disappear in trees that are just one step longer. These are not as well supported as clades that persist even in all trees that are several or many steps longer than the MPTs. The decay index is the length of the shortest tree that does not include a particular clade minus the length of the shortest tree that does include the clade. It is a commonly used measure of support for clades in MPTs and helps to identify the strengths and weaknesses of the tree (Donoghue *et al.* 1992).

Bootstrapping is another technique that provides measures of support for particular clades (Felsenstein 1985). Numerous bootstrap replicate datasets are produced by random resampling with replacement of characters from the original dataset. Each bootstrap dataset has the same number of characters as the original data but each of the original characters may be represented once, more than once, or not at all in each replicate. This is conceptually like randomly reweighting the original characters. Each replicate is analysed and the proportion of analyses that yield MPTs that include a particular clade is taken as a measure of support for that clade. Bootstrap proportions have uncertain statistical properties, particularly in the context of phylogenetic analysis of morphological data, and interpreting them as strict confidence intervals is unwarranted. However, bootstrapping provides a useful indicator of the relative levels of support for different clades, as indicated by their robustness in the face of random perturbations in character weights.

Of course, high bootstrap proportions and decay indices can result from abundant and perhaps correlated homoplasy or the overweighting of some similarity by dividing it into many separate characters. Thus high values are not a necessary indicator of accuracy. Unfortunately, the instability of taxa that have little data, such as highly incomplete fossils, can mask the strength of support for other relationships, as measured by bootstrap proportions or decay indices.

Where bootstrap proportions and/or decay indices are low, the quality of the data upon which the phylogenetic hypothesis is based must be suspect. Parsimony analysis will yield trees even when the data are random with respect to phylogeny. Randomization tests compare some measure of the quality of the original data, such as tree length, with the distribution of the same measure obtained with similar but phylogenetically uninformative data. The latter are prepared by randomly permuting the assignment of data points to taxa within each character. This reduces any congruence between characters to that expected by chance alone, and allows the null hypothesis that the original data are indistinguishable from random to be tested (Faith and Cranston 1991). Little confidence should be invested in relationships inferred from data for which the null hypothesis cannot be rejected.

Conclusion

The science of numerical phylogenetic analysis continues to be an area of rapid growth in methods, measures, and results. More simulation and other studies aimed at determining the properties of the burgeoning array of methods are needed. Fundamental philosophical issues continue to divide the discipline. Of more practical importance are the challenges that remain for the integration of palaeontological and neontological phylogenetics (much of the latter based on macromolecular sequence data), and for coping with the effects of the highly incomplete data and unstable taxa with which palaeontologists often work.

References

Donoghue, M.J., Olmstead, R.G., Smith, J.F. and Palmer, J.D. (1992) Phylogenetic relationships of Dipsacales based on rbcL sequences. *Annals of the Missouri Botanical Garden* **79**, 333–345.

Faith, D.P. and Cranston, P.S. (1991) Could a cladogram this short have arisen by chance alone? On permutation tests for cladistic structure. *Cladistics* **7**, 1–28.

Felsenstein, J. (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39**, 783–791.

Gingerich, P.D. (1979) The stratophenetic approach to phylogeny reconstruction in vertebrate paleontology. In: J. Cracraft and N. Eldredge, eds. *Phylogenetic analysis and*

paleontology, pp. 41–77. Columbia University Press, New York.
Maddison, W.P., Donoghue, M.J. and Maddison, D.R. (1984) Outgroup analysis and parsimony. *Systematic Zoology* **33**, 83–103.
Swofford, D.L. and Begle, D.P. (1993) *PAUP: Phylogenetic Analysis Using Parsimony*, *Version 3.1*. User's Manual. Smithsonian Institution, Washington, DC.
Swofford, D.L., Olsen, G.J., Waddell, P.J. and Hillis, D.M. (1996) Phylogenetic inference. In: D.M. Hillis, C. Moritz and B.K. Mable, eds. *Molecular systematics*, 2nd edn, pp. 407–514. Sinnauer Associates, Sunderland, Massachusetts.
Wilkinson, M. (1995) A comparison of two methods of character construction. *Cladistics* **11**, 297–308.
Wilkinson, M. and Benton, M.J. (1996) Sphenodontid phylogeny and the problems of multiple trees. *Philosophical Transactions of the Royal Society of London B* **351**, 1–16.

5.3.2 Fossils in the Reconstruction of Phylogeny

P.L. FOREY and R.A. FORTEY

Introduction

Fossil evidence has traditionally played a central role in the reconstruction of phylogeny for groups of organisms with a good fossil record, but more recently that role has been re-examined (Patterson 1981). There is no question that fossils afford the only direct evidence of the remote history of clades. Debates about their use in phylogeny tend to focus on the question of how much the incorporation of fossil evidence alters phylogenetic histories reconstructed on the basis of living organisms alone, for which almost limitless evidence can be derived from molecular and soft-anatomy sources. These kinds of data are almost unavailable from fossils.

Theories of descent

Phylogenies based upon living organisms do not attempt to restore an historical 'tree of descent' but are concerned with recency of common ancestry as revealed by the distribution of homologous characters, usually analysed cladistically. However, there are many clades of organisms with an excellent fossil record—especially those which have no close living relatives—and, for these, fossils in their stratigraphic context have been much used in erecting theories of descent. In general, groups with relatively complete records (e.g. ammonites, foraminifera, and graptolites) are those for which phylogenetic hypotheses are best constructed in this fashion. Vertebrate examples with the same resolution of record are unusual, but early Tertiary mammals from the Bighorn Basin, Montana, were sufficiently well known to allow their phylogeny to be analysed with stratigraphic and morphological data (the stratophenetic method: see Polly 1997). Such complete records usually prevail for relatively brief time periods (typically a chronostratigraphic stage or two); hence the phylogenies resulting are concerned with phyletic relationships at a low level in the taxonomic hierarchy (species and genera). Questions of high-level phylogeny are less amenable to this approach. In spite of their comparative rarity, stratophenetic examples are significant since upon their reality depend case histories of palaeobiological importance, such as those contrasting gradualistic change with punctuated equilibria.

Possibly the best examples of phylogenetic hypotheses derived only from fossils are found among planktic foraminiferans. The Miocene lineage *Globigerinoides triloba–G. sicanus–Praeorbulina glomerosa–Orbulina universa* (Fig. 5.3.2.1a) is known from dozens of rock sections, and embodies a complex series of morphological changes as the final whorl progressively embraces the earlier one; it is often claimed as an example of gradualistic change. The taxonomic treatment in this case is entirely incompatible with cladistic treatment of the same organisms, since (part of) the genus *Globigerinoides* effectively 'gives rise' both to *Praeorbulina* and then to *Orbulina*, and the first two named are therefore a paraphyletic group (Fig. 5.3.2.2a). Such a contrast in taxonomic designation depending on the kind of phylogenetic approach adopted is the result of explicit recognition of ancestors in historical trees of descent.

A second example of the historical approach to phylogenetics is afforded by Ordovician graptolites (Cooper and Ni 1986) (Fig. 5.3.2.1b) with a distinctive isograptid development. As with the foraminiferan example, the succession of species has been confirmed in several successions worldwide, but the tree also includes branching events. Quantitative assessment of variation and transformation between certain species of *Isograptus* and *Pseudisograptus* makes this one of the more thoroughly treated examples, which does not depend solely on subjective judgements of ancestral and descendant states (for which this historical method has been criticized). When the relationships are portrayed as a cladogram, the paraphyletic nature of *Pseudisograptus* is revealed (Fig. 5.3.2.2b).

Unknown character combinations

In the more general context of high-level phylogenetic analysis, fossils—particularly ancient ones—are likely to show character combinations which are no longer

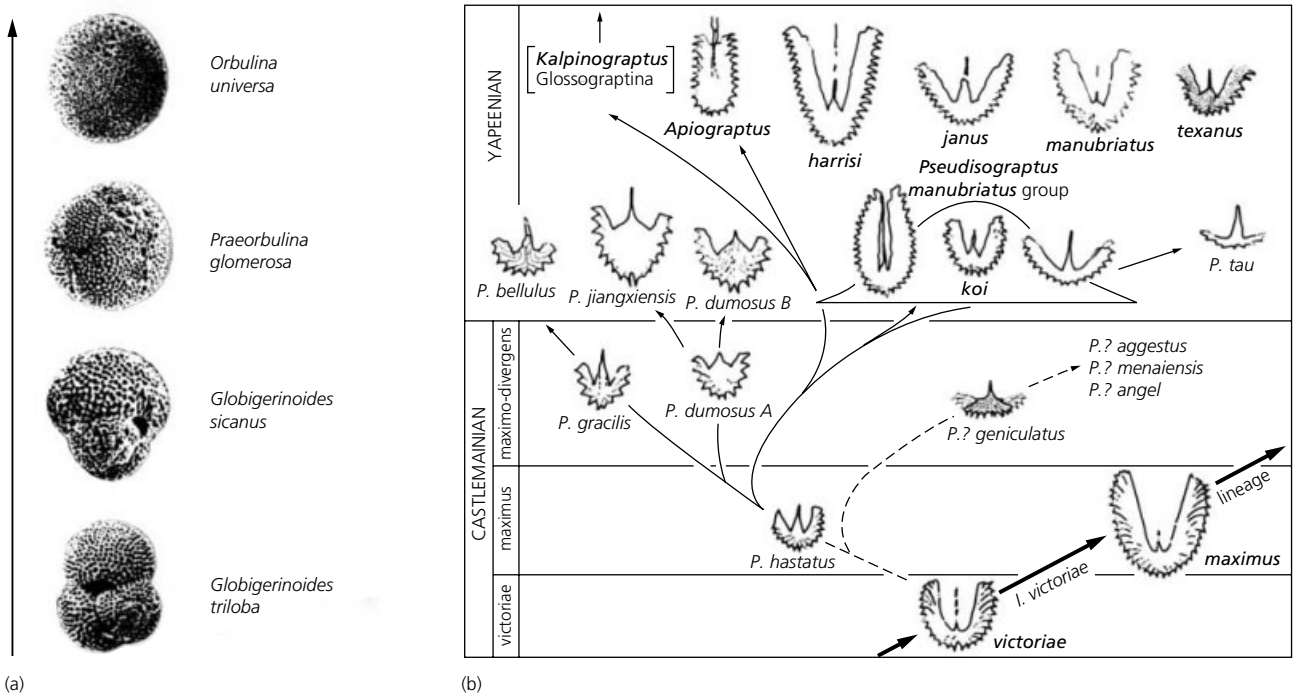

Fig. 5.3.2.1 (a) Hypothesized anagenetic lineage of Miocene planktic foraminiferans leading to the cosmopolitan form *Orbulina universa*, wherein one species is thought to have given rise to successive daughter species. (b) Phylogenetic tree of isograptid graptolites which includes both hypothesized ancestor–descendant relationships as well as cladogenetic events. Both of these examples of tree building are based on repeatable observations of the different morphologies in several geological successions. (a, Photographs courtesy of J.E.P. Whittaker; b, from Cooper & Ni 1986.)

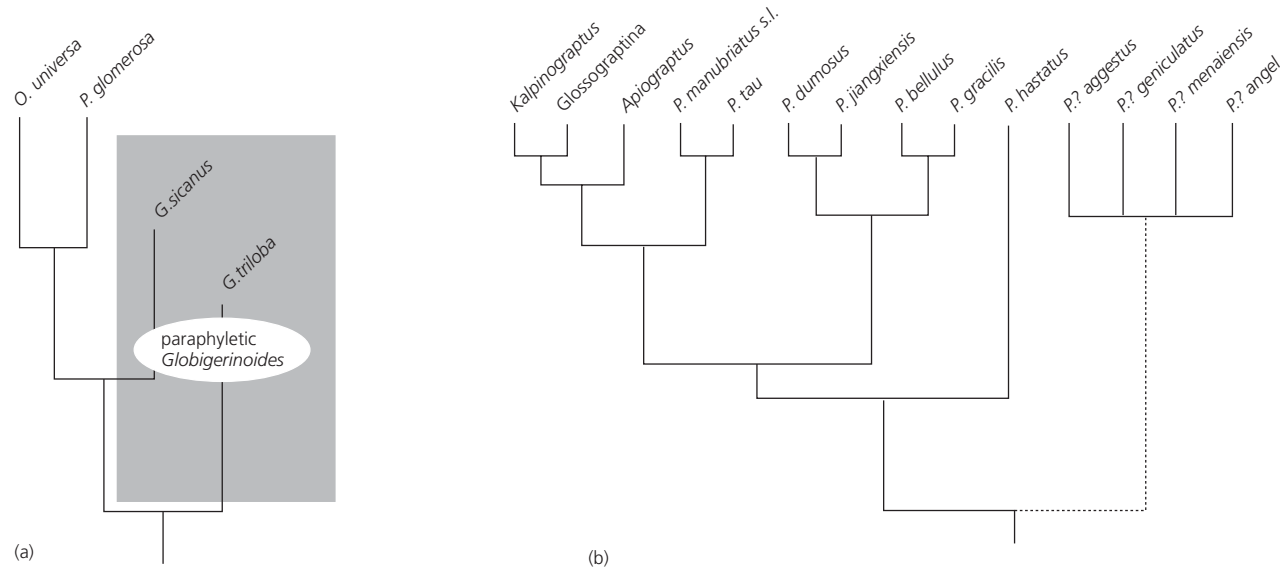

Fig. 5.3.2.2 Cladistic representations of the phylogenies shown in tree form in Fig. 5.3.2.1. (a) Planktic foraminiferal lineage represents *Globigerinoides* as a paraphyletic taxon, which is unacceptable in cladistic terms. (b) Graptolite cladogram shows that the genus *Pseudisograptus* 'lumps' all primitive members of the major clade, while including two smaller clades within it.

present in living forms. This can be important if characters present in fossils but lost or modified in living taxa serve to identify hitherto unsuspected sister-groups. An example is the Cambrian marine arthropod *Canadaspis perfecta*, which has been interpreted as a crustacean on the basis of the structure and homology of the limbs, even though at least one appendage pair normally incorporated into the crustacean head remained in the front of the thorax. If this interpretation is correct, it reveals a whole range of Cambrian taxa with this kind of cephalic construction as possible sister-groups, and thereby contributes to our knowledge of the origins of a major group. Similarly, the Cambrian lobopod *Aysheaia* was capable of subaqueous respiration, indicating that the marine habitat was primitive for the group (all living lobopods are terrestrial) and permitting new ways of accommodating these animals among the stem arthropods. In the same way, the fusion of the palate to the braincase in tetrapods and lungfishes was assumed to be a homologous character—but fossils of both groups show a free (unfused) condition, and reveal that the fusion is the result of parallel evolution and a false guide to the relationship between the Recent taxa.

The interpretation of homology of structures in fossils is often controversial, not least because their preservation is often imperfect. Many specialists disagree, for example, on the interpretation of appendages concerned with major features of insect evolution (compare Kukalova-Peck with Willman and Kristansen *in* Fortey and Thomas 1997). In the most extreme cases even the basic orientation of fossils can be controversial (e.g. calcichordates, *Hallucigenia*), such that there is little agreement about dorsal/ventral or anterior/posterior and this makes it difficult to describe the head or tail, or left or right. More usually, there are difficulties in restoring soft parts of fossils known only from the skeleton. In these circumstances the interpretation of morphological structures depends upon the choice of a Recent model, a choice ideally justified by demonstrating unambiguous synapomorphies between the fossil and the chosen Recent template.

Older taxa within fossil groups which lack a close modern template—as opposed to those from younger strata—may be of particular service in the interpretation of relationships. Advanced ammonoids have highly complex suture patterns, whereas Devonian ones are both comparatively simple and show homologies with nautiloid contemporaries. Early Cambrian olenellid trilobites lack the dorsal facial sutures which are common among later trilobites, and thus become the best trilobites to compare with soft-bodied contemporaries such as the recently discovered Early Cambrian xandarellids, which also lack dorsal sutures of advanced trilobite type. Stratigraphically early planktic graptoloids retain bithecae, which are lost in all advanced graptoloids, but suggest comparisons with dendroid graptolites. These comparisons further identify the sicula carrying a delicate thread, the nema, as a crucial autapomorphy for definition of the Graptolithina.

The inclusion of fossils in phylogenetic analyses may help to resolve disputes among competing theories based solely on Recent organisms. For example, there are two competing theories specifying the phylogenetic position of hyraxes (rock rabbits), one of which places them as the sister-group to horses, the other as the sister-group to elephants and sea cows (Novacek 1994). The inclusion of fossil taxa introduced unique character combinations and resolved the ambiguity in favour of the first alternative. A different kind of example is the two equally parsimonious solutions of the phylogenetic relationships of Recent echinoids based on the analysis of large subunit ribosomal RNA. Analysis of the fossil members of the lineages leading to the terminal taxa sampled for the molecules showed that one of the two hypotheses required fewer assumptions about the incompleteness of the fossil record and may therefore be preferred (Smith and Littlewood 1994).

Fossils may also provide a realistic root for a phylogenetic analysis which requires a taxon to provide a starting point for ideas of character change, particularly in clades which have separated from their Recent sister-group deep in geological time. It is very difficult to polarize much of the morphological variation in asteroids by using Recent ophiuroids as the outgroup since modern brittlestars are highly autapomorphic (Smith 1997). Instead, the use of a stem-group fossil such as *Strataster* provides a closer morphological starting point.

Aside from the influence that fossils may have on the topological relationships between Recent taxa, fossils have important roles to play in the reconstruction of character evolution, which is another dimension of phylogenetic reconstruction. In this context the inclusion of fossils may be crucial in two ways: (1) by stabilizing theories of character evolution; and (2) by clarifying the sequence of character changes leading to the acquisition of complex morphologies. The first is shown by the evolution of the gills within vertebrates. The jawless fishes, hagfishes and lampreys, which are successive sister-groups to jawed vertebrates (gnathostomes), each have pouch-like gills opening to the outside through pores rather than the slit-like gills in gnathostomes, most visibly demonstrated in sharks. Such gill morphology has implications for the way that they are ventilated. Given this information, we would be undecided whether the pouch-like gills were primitively present in vertebrates and subsequently transformed to slit-like gills in gnathostomes, or if pouch-like gills were independently derived in hagfishes and in lampreys. The incorporation of fossil jawless fishes into a phylogeny of vertebrates, all of which have pouch-like gills, clearly

demonstrates that the primitive vertebrate gills were pouch-like.

An example of the fossil record helping to understand the evolution of complex morphologies is exemplified by the evolution of the tail of a teleost fish. The endoskeleton of the teleost tail is a complex structure with modified haemal spines (hypurals) supporting most of the fin rays and modified neural arches (uroneurals) which reach forward as splint-like braces to strengthen the tail skeleton. This type of tail appears much more complicated than that in the modern sister-group where the endoskeleton is developed as a gradual upturning of the end of the vertebral column, with little modification of either neural arches or haemal spines. With just these two morphologies it would be difficult to imagine the stages by which one transformed into the other. However, the inclusion of stem-lineage teleosts shows that there are sequential changes affecting different parts of the endoskeleton at successive cladogenetic events leading to the abbreviated and strengthened tail of the modern teleost (Fig. 5.3.2.3).

Although there are many advantages to including fossils in phylogenetic reconstructions, there is one major disadvantage. Fossils are always incomplete organisms and in modern phylogenetic analyses (phenetic or cladistic) their inclusion means that many characters scorable in Recent taxa are unknown and must be entered as question marks. Such codings can cause computational problems and result in poorly resolved hypotheses. Some methods have been developed to alleviate the effects of poorly known fossils (Wilkinson and Benton 1995) but they sacrifice some fossils on the altar of precise phylogeny reconstruction. The 'ledger sheet' for the use of fossils in phylogeny is summarized in Table 5.3.2.1.

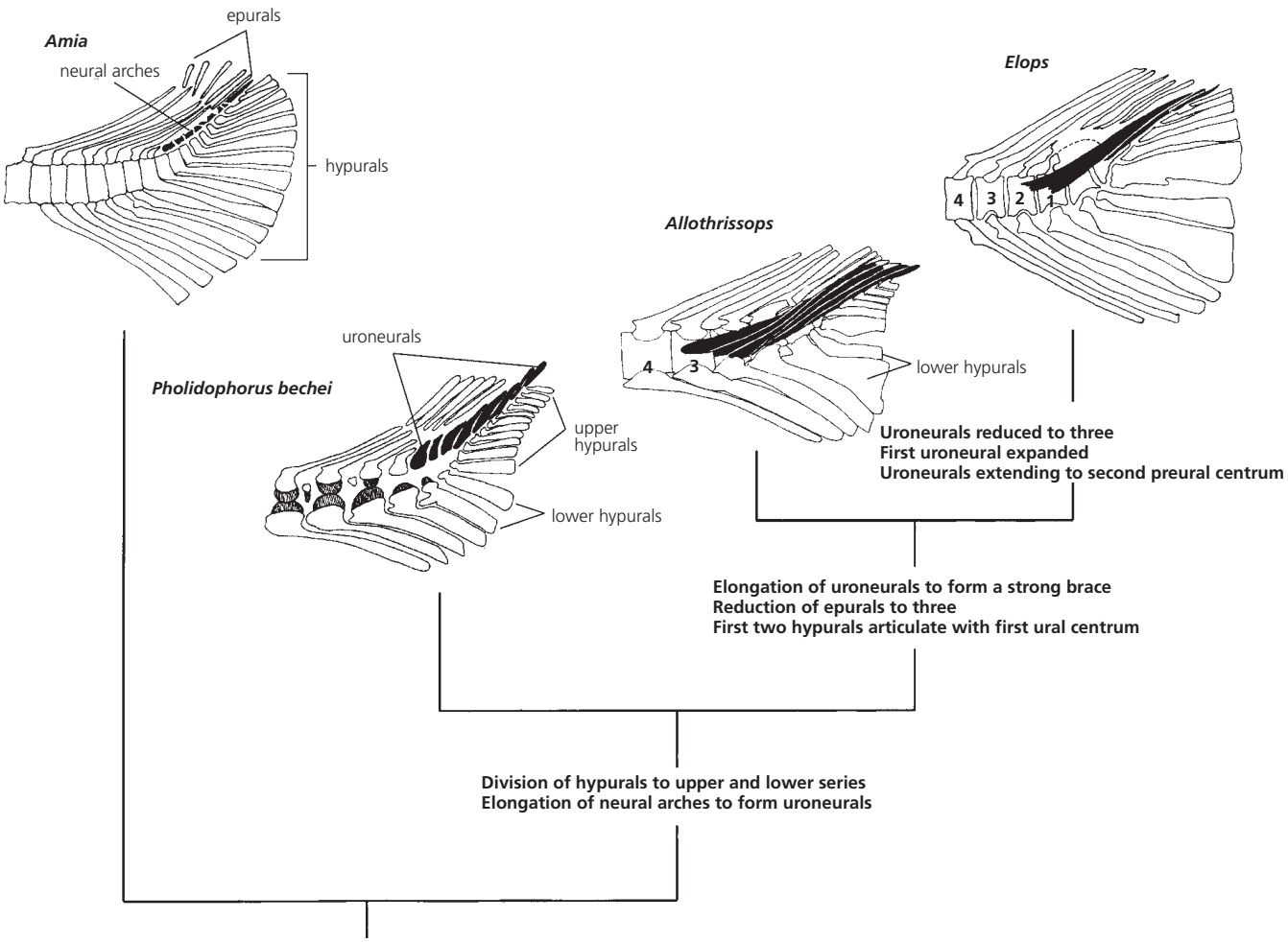

Fig. 5.3.2.3 The modern teleost tail, such as that of *Elops*, is a complex structure formed by highly modified neural and haemal arches, in contrast to the relatively simple tail of the living sister-group, *Amia*. Consideration of the tail structure of fossil teleosts, such as *Pholidophorus bechei* and *Allothrissops*, shows that there was a sequential acquisition of the characters listed here against nodes on the phylogenetic tree.

Table 5.3.2.1 Uses of fossils in phylogeny.

Fossils as additional taxa with unique combinations of characters:
1 break up long branch lengths of molecular trees and may provide more suitable outgroups
2 stabilize uncertain polarities of character evolution
3 arbitrate between theories based on living organisms
4 determine sequences of events leading to complex morphologies
Fossils with their time component:
5 can arbitrate between 'modern' theories by using stratigraphic occurrence
6 determine minimum ages of origin and ages of differentiation (useful for calibrating molecular clocks)
7 allow comparison between cladogenesis with theories of Earth history
8 can be used to propose theories of coevolution (e.g. insects and plants, hosts and parasites)

References

Cooper, R.A. and Ni, Y.-N. (1986) Taxonomy, phylogeny and variability of *Pseudisograptus* Beavis. *Palaeontology* **29**, 313–363.

Fortey, R.A. and Thomas, R.H., eds. (1997) *Arthropod relationships*. Systematics Association Special Volume no. 55. Chapman and Hall, London.

Novacek, M.J. (1994) Fossils as critical data. In: M.J. Novacek and Q.D. Wheeler, eds. *Extinction and phylogeny*, pp. 46–88. Columbia University Press, New York.

Patterson, C. (1981) Significance of fossils in determining evolutionary relationships. *Annual Review of Ecology and Systematics* **12**, 195–223.

Polly, P.D. (1997) Ancestry and species definition in paleontology: a stratocladistic analysis of Paleocene–Eocene Viverravidae (Mammalia, Carnivora) from Wyoming. *Contributions from the Museum of Paleontology, University of Michigan* **30**, 1–53.

Smith, A.B. (1997) What does palaeontology contribute to systematics in a molecular world? *Molecular Phylogenetics and Evolution* **9**, 437–447.

Smith, A.B. and Littlewood, D.T.L. (1994) Palaeontological data and molecular phylogeny analysis. *Paleobiology* **20**, 259–273.

Wilkinson, M. and Benton, M.J. (1995) Missing data and rhynchosaur phylogeny. *Historical Biology* **10**, 137–150.

5.3.3 Stratigraphic Tests of Cladistic Hypotheses

M.A. NORELL

Introduction

Can the fossil record provide a test of cladistic hypotheses? The history of life as read from the rocks, given an adequate fossil record, should correspond with that history recovered from cladistic analysis. A number of issues complicate this relationship, including taphonomy, preservational biases, and the problem of asymmetric character evolution following splitting of lineages (where one lineage evolves novel, diagnosable characters which distinguish it from the ancestral condition before its sister-lineage) (Norell 1992). Yet the question whether or not the fossil record is precise enough to provide rigorous tests of cladistic analyses still exists.

Before any test can be applied to either the stratigraphic record or to a cladistic phylogeny, what is meant by a test needs to be clarified. Here two types of tests, 'soft' and 'hard', are recognized. Soft tests are those that may give more support to a particular hypothesis. As used here, soft tests may help distinguish between sets of most parsimonious trees. A tree, or set of trees, may be preferred because it corresponds with other data (superpositional relationships). In such cases stratigraphic relationships are not used as an optimality criterion, in that the original set of phylogenetic trees recovered from cladistic analysis cannot be overturned. Conversely, hard tests implicitly use stratigraphic relationships, usually in combination with character data, and may overturn hypotheses of relationship based exclusively on characters. This means that trees with suboptimal lengths are preferred.

Hard tests

The use of stratigraphic data as a method of phylogeny reconstruction has a long history in palaeontology. Recently a host of new methods incorporate stratigraphic information into the construction of the initial phylogeny. Because these analyses may produce phylogenetic trees that are at odds with those constructed from parsimony alone, they constitute hard tests. These methods fall into two categories: ones which are in some sense parsimony based and those based on likelihood.

Methods have been proposed which introduce stratigraphic data into a data matrix by adding stratigraphic characters to the morphological data (see Clyde and Fisher 1997 for citations). From this a stratigraphic parsi-

mony debt is calculated which corresponds to the minimum number of stratum crossings required by the resultant topology. If this stratigraphic parsimony debt is great enough, it can override morphology and influence tree topology. Unfortunately, 'the weight the stratigraphic data receive can be arbitrarily increased or decreased by considering more or fewer stratigraphic zones, respectively' (Huelsenbeck and Rannala 1997, p. 179).

Comparison of retention indices of stratigraphic and character data has been analysed under several types of topological constraint (Clyde and Fisher 1997). This has shown that, according to mixed optimality criteria, trees which deviate from the most parsimonious tree, both topologically and in allowance of ancestral taxa, may be equally or better supported than the shortest character trees. This phenomenon can be summarized as 'Significant gains in stratigraphic fit can be realized without significant loss in morphologic fit as the stratigraphic and morphologic evidence are both allowed to participate in constraining the structure of phylogenetic hypotheses' (Clyde and Fisher 1997, p. 1).

Another type of algorithm (Wagner 1995) examines taxa sister-group by sister-group, asking the question: are these nodes stratigraphically compatible? This procedure (Fig. 5.3.3.1) explicitly requires taxa to be considered ancestors simply because of the stratigraphic position of their sister-group. Implementation of this algorithm often requires trees of suboptimal length to be preferred, because taxa must occasionally de-evolve characters to make them suitable ancestors (Wagner 1995). Reweighting schemes have also been proposed which can be described as 'some measure of stratigraphic consistency is used to reweight parsimony trees to find the tree most consistent with all of the data' (Wagner 1997, p. 120).

These procedures suffer from several pitfalls, a notable one being the mixing of optimality criteria to include both stratigraphic signal (a linear process) and phylogeny (a hierarchical process). Incorporating stratigraphic criteria into such an analysis (as in Stratigraphic Parsimony) confounds optimality criteria, because it assumes that temporal equivalency is a homology statement in the same way as the correspondence between morphological character states. Several other criticisms of these methods have been aired (see Huelsenbeck and Rannala 1997, among several others).

More generally, these approaches cannot actually test a cladistic phylogeny because they are not independent, as they too are based explicitly on the same set of charac-

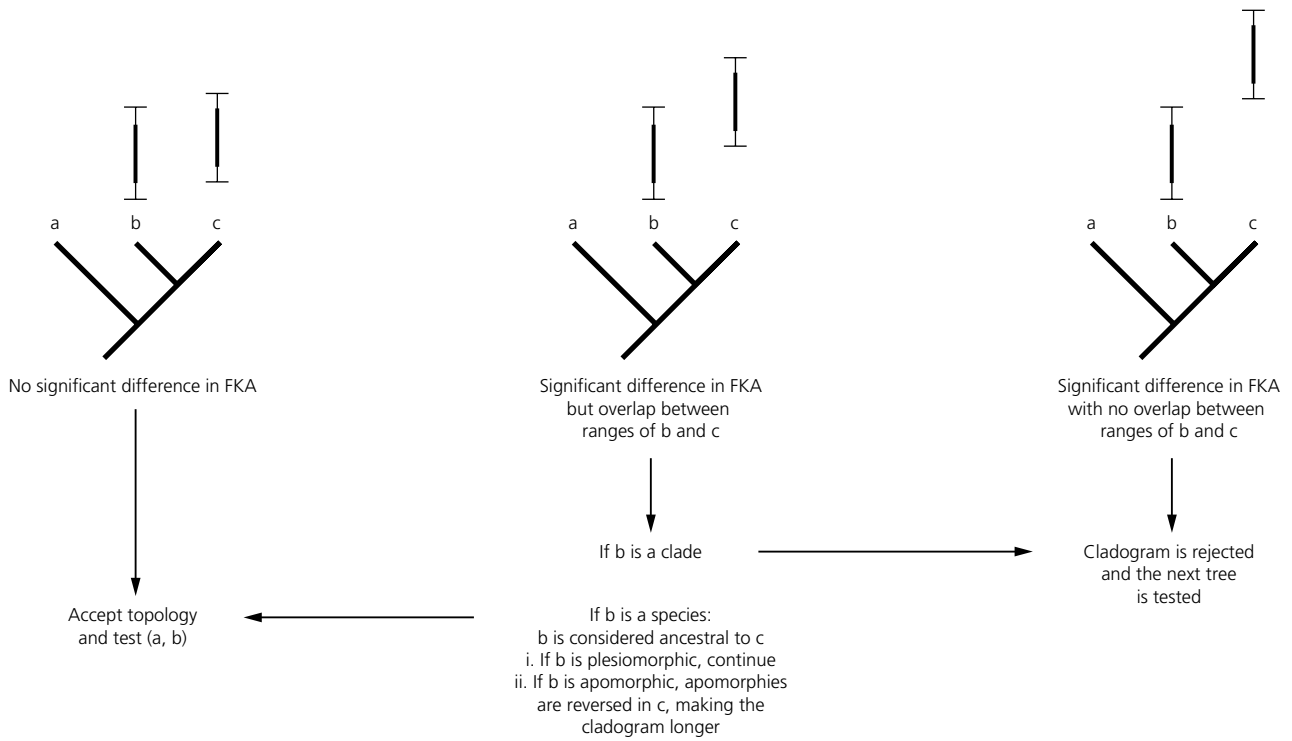

Fig. 5.3.3.1 Algorithm which may result in the acceptance of trees that are longer than optimal; for a complete discussion see Wagner (1995, p. 159). Differences in first known appearance (FKA) can modify topologies based on character data or force species into becoming ancestors (these are then required to 'de-evolve' any diagnostic apomorphies). (Modified from Wagner 1995.)

ters. In this sense no pure method (i.e. one totally divorced from phylogeny) has been proposed, since all are dependent on initial grouping criteria (based on morphology) to identify the groups and delimit taxa. Because it will be difficult to get beyond using initial grouping criteria to delimit groups, a better approach may be a nihilistic one where no taxa are recognized a priori, only specimens. These specimens are then ordered by stratigraphy and characters into a phylogeny. This allows characters that place individual specimens into taxa to de-evolve as readily as characters that are used to identify higher groups. In doing so it allows specimens that are morphologically identical to be placed in different taxa.

A likelihood procedure which constructs a phylogeny via a model of fossil preservation has been proposed (Huelsenbeck and Rannala 1997). This method is divorced from character evidence beyond initial grouping criteria. The likelihood model is optimized against gaps in the fossil record and assumes that 'the rate of preservation of lineages in the rock record over time is assumed to be constant and is therefore a Poisson process' (Huelsenbeck and Rannala 1997, p. 175). This is a very simple model and it is cautioned that 'the stratigraphic record is limited for most groups and the estimates of phylogeny using stratigraphic methods are biased for low preservation rates; stratigraphic methods may not be best suited for estimating phylogeny without additional data from other sources' (ibid.).

Soft tests

Unlike the cases described above, soft tests generally are indices of how well a phylogeny performs relative to a fossil record. These metrics are generated by comparing fit between a cladistic hypothesis and some aspect of the fossil record. Two sorts of indices have been proposed: (1) indices measuring order of cladistic branching vs. the appearance of fossils in the stratigraphic column; and (2) indices measuring amount of missing time predicted by a phylogenetic tree.

Initially, the relationship between a cladistic tree and stratigraphy was explored in a study which assessed the importance of fossils in phylogeny reconstruction (Gauthier *et al.* 1988). Comparisons were made between the order of fossil occurrence in the geological record and the order of branching from the bottom node of a cladogram using a non-parametric correlation procedure. Later these methods were refined (Norell and Novacek 1993) and similar and derivative methods applied (Benton and Storrs 1996, among others).

Although never used as a direct test of cladograms, these methods were employed to determine how correspondent a fossil record was with a phylogeny (e.g. Norell and Novacek 1993). Such approaches suffer from a number of difficulties, the most serious being that only pectinate trees can be examined (Siddall 1998). Consequently trees with secondary structure need to be reduced to pectinate elements for analysis (e.g. Norell and Novacek 1993).

Huelsenbeck (1994) recognized these difficulties and proposed the Stratigraphic Consistency Index (SCI). This index is a measure of how many nodes in a tree are consistent with stratigraphy compared with how many are not, divided by the total number of nodes. This test also has difficulties, the primary one being that it is biased towards trees with pectinate shapes (Siddall 1996).

A different approach has been to use a direct index of fit between a stratigraphic record and phylogeny, usually by creating an index based on the magnitude of gaps in the record. In general these approaches evaluate, sum, or average the lengths of ghost lineages (see Norell 1992) over entire trees, preferring those trees that minimize the lengths of ghost lineages (Fig. 5.3.3.2). Several of these have been presented (see Norell 1992; Benton and Storrs 1996, among others). Unfortunately, comparisons among records of different scales or among datasets are problematic (Norell 1992). All are also somewhat

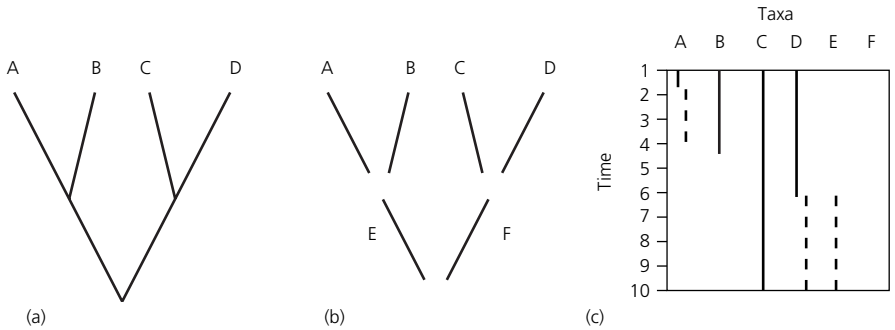

Fig. 5.3.3.2 Individual lineages are recognized (b) from the phylogeny in (a). Lineages are calibrated using the fossil record in (c) (solid bars). Resultant ghost lineages for taxa A, D, and E that are predicted by the fossil record and the phylogenetic hypothesis are plotted as dashed bars in (c); for a complete discussion see Norell (1992, 1993). (Modified from Norell 1993.)

flawed in that there are (at least potentially) implicit biases concerning tree shape. This is probably a reflection of the nature of the two patterns and their underlying processes: temporal position is linear while phylogeny is hierarchical.

A creative alternative, the Manhattan Stratigraphic Measure (MSM), has been presented which 'uses the Manhattan distance between stratigraphic ages to determine fit to a tree' (Siddall 1998, p. 201). This is accomplished by calculating Manhattan distances between all terminal taxa and optimizing these distances on the shortest tree to calculate a length. In itself, this length is not comparable among trees; however, it can be compared with the minimum possible length, calculated by deriving a tree that optimizes the Manhattan matrix. The MSM is the difference between this minimum length and the length of the original tree. This method is 'not biased by tree shape, it is sensitive to the magnitude of age discrepancy and there is an obvious significance test' (Siddall 1998, p. 201). This significance test is constructed via permutation where a distribution of potential MSMs is calculated from randomly derived trees. A calculated *P*-value is based on how well the observed MSM performs against these randomly derived MSMs.

Conclusion

Why are these methods necessary? Two things come to mind. The first is that stratigraphy, as an independent source of phylogenetic information, may inform phylogeny; the second is that these methods may be useful in evaluating the quality of specific fossil records.

So far, only a weak case has been made that these methods inform phylogeny. Only by implementing additional, hard to justify, assumptions (estimators of fossil preservation, ancestors, etc.) and mixing optimality criteria does this make sense. Instances where success has come through conflating assumptions and mixing optimality criteria are difficult to identify and need to be evaluated critically.

The utility of these methods (specifically the MSM) probably lies in evaluating the quality of specific fossil records. The contemporary literature is full of articles attaching evolutionary processes or catastrophic events to patterns in the fossil record. Do these records capture life's history with enough veracity to allow such interpretation? Unfortunately we do not know—minimally these records should be highly congruent with our best estimation of phylogeny derived from independent means.

References

Benton, M.J. and Storrs, G.W. (1996) Diversity in the past: comparing cladistic phylogenies and stratigraphy. In: M.E. Hochberg and R. Barbault, eds. *Aspects of the genesis and maintenance of biological diversity*, pp. 19–40. Oxford University Press, New York.

Clyde, W.C. and Fisher, D.C. (1997) Comparing the fit of stratigraphic and morphologic data in phylogenetic analysis. *Paleobiology* **23**, 1–20.

Gauthier, J., Kluge, A.G. and Rowe, T. (1988) Amniote phylogeny and the importance of fossils. *Cladistics* **4**, 105–209.

Huelsenbeck, J.P. (1994) Comparing the stratigraphic record to estimates of phylogeny. *Paleobiology* **20**, 470–483.

Huelsenbeck, J.P. and Rannala, B. (1997) Maximum likelihood estimation of phylogeny using stratigraphic data. *Paleobiology* **23**, 174–180.

Norell, M.A. (1992) The effect of phylogeny on temporal diversity and evolutionary tempo. In: M.J. Novacek and Q.D. Wheeler, eds. *Extinction and phylogeny*, pp. 89–118. Columbia University Press, New York.

Norell, M.A. (1993) Tree based approaches to understanding history: comments on ranks, rules and the quality of the fossil record. *American Journal of Science* **293A**, 407–417.

Norell, M.A. and Novacek, M.J. (1993) Congruence between superpositional and phylogenetic patterns: comparing cladistic patterns with fossil records. *Cladistics* **8**, 319–338.

Siddall, M.E. (1996) Stratigraphic consistency and the shape of things. *Systematic Biology* **45**, 111–115.

Siddall, M.E. (1998) Stratigraphic fit to phylogenies: a proposed solution. *Cladistics* **14**, 201–208.

Wagner, P.J. (1995) Stratigraphic tests of cladistic hypotheses. *Paleobiology* **21**, 153–178.

Wagner, P.J. (1997) Patterns of morphologic diversification among Rostroconchia. *Paleobiology* **23**, 115–150.

5.3.4 Molecular Phylogenetic Analysis

J.P. HUELSENBECK

Introduction

With the more widespread use of molecular data for phylogeny reconstruction, there is increased concern with the potential conflict between molecules and morphology. Many systematists were concerned that trees estimated from morphological data might be incongruent with those estimated from molecular data. A closely related question was the role that fossils play in phylogenetic analysis. Given that fossils only provide a limited number of morphological characters, can they meaningfully contribute to a phylogenetic analysis that includes a mixture of living and fossil species? Although counterexamples can always be found, the emerging consensus is that: (1) in many cases trees constructed using morphology and molecules are congruent; and (2) fossils can

play an important role in phylogenetic analysis because they often preserve unique combinations of characters not present in living species. Moreover, fossils provide information on the timing of major events—a type of information completely lacking with other forms of data. When fossil information is combined with molecular data, the types of inferences that can be made exceed those based on either dataset in isolation. For example, a combination of molecular and palaeontological data can be used to date speciation events for groups that have a poor fossil record. The fossils are used to calibrate a molecular clock for a particular gene. This calibration, along with the assumption of a molecular clock, allows other speciation events to be dated.

A variety of methods are available for estimating phylogeny from molecular data. Here, the focus is on model-based methods of phylogeny estimation. Model-based approaches for the analysis of molecular data have become more practical as computer speed has improved and the stochastic models that form the heart of these methods have been elaborated to reflect biology more closely.

Molecular data

Only amino acid and DNA sequences are considered here (other types of molecular data, such as allozymes or microsatellites are not discussed). The data are treated as an aligned matrix of sequences, such as the following DNA sequence matrix:

Taxon 1	TTT	CCT	AAT	AGT	TCT
Taxon 2	TTT	CCC	AAT	AGT	TCT
Taxon 3	TTC	CCC	AAC	AGA	TCG
Taxon 4	TTC	CCA	AAC	AGA	AGT
Taxon 5	TTT	CCG	AAC	AGG	AGC

or the corresponding amino acid matrix

Taxon 1	Phe	Pro	Asn	Ser	Ser
Taxon 2	Phe	Pro	Asn	Ser	Ser
Taxon 3	Phe	Pro	Asn	Arg	Ser
Taxon 4	Phe	Pro	Asn	Arg	Ser
Taxon 5	Phe	Pro	Asn	Arg	Ser

Although the data are presented as an aligned matrix of amino acids or nucleotides, it should be remembered that these matrices are not the actual observations made by the biologist; the observations are the individual sequences, not the aligned matrix. Ideally, phylogenetic methods should treat the data as the individual sequences and simultaneously estimate the alignment and phylogenetic tree. Simultaneous alignment and phylogenetic analysis are currently implemented only with the maximum parsimony method (e.g. MALIGN: Wheeler and Gladstein 1994). Phylogenetic analysis of molecular data largely remains a two-step procedure: sequence alignment followed by phylogenetic analysis.

Models and phylogenetic inference

All phylogenetic methods, of necessity, make assumptions about the evolutionary processes that generated the observed data, e.g. that species share an (unknown) history that can be modelled as a bifurcating tree. Many methods, such as distance, maximum-likelihood, and Bayesian methods (see 'Estimating phylogeny', p. 526), also make explicit assumptions about the process of DNA or amino acid change in the form of a stochastic model of substitution.

Even maximum parsimony, probably the most agnostic method of phylogenetic inference, makes assumptions about the process of DNA or amino acid substitution. The parsimony method accommodates unequal rates of change by assigning weights to different sites or between different character states. For example, a common observation in comparison of DNA sequences is that transitions (A ↔ G or C ↔ T changes) occur much more frequently than transversions (A ↔ C, A ↔ T, C ↔ G, or G ↔ T changes). In a parsimony analysis, more importance can be assigned to the rare changes by weighting transversions more heavily than transitions. Another common observation is that rates of substitution vary across a sequence. For example, the rate of substitution is typically lowest at second codon positions, followed by the first and third codon positions (the third position has the highest rate of substitution). (The first, second, and third codon positions refer to the first, second, and third base in the triplet of bases that encode a particular amino acid.) This pattern makes sense in the light of the genetic code and can be accommodated in a parsimony analysis by assigning different weights to different positions in the sequence. The goal is to give more weight to the rare changes than to the common ones, on the assumption that rare changes are more informative about phylogeny (i.e. are less prone to homoplasy).

One of the problems with the weighting approach in a parsimony analysis is that there is no clear guide to what the exact weights should be. Several different approaches have attempted to choose optimal weights based on the data. Most molecular systematists examine whether the weighting scheme applied makes a significant difference to the estimated phylogenetic tree. If the trees obtained using several different weighting schemes are the same, or very similar, this is taken as evidence that the analysis is robust to choice of weighting schemes.

Another approach that has been successfully applied to molecular data is to model substitutions as a stochastic process. There are several advantages of such an approach. First, parameters can be directly estimated from the data using several standard statistical methods. In many cases the parameters of models of substitution are of biological significance (such as the rate of DNA substitution, the transition/transversion rate ratio, or

the rate of non-synonymous and synonymous substitution (non-synonymous changes in a protein-coding DNA sequence change the amino acid sequence of the protein whereas synonymous changes do not), so that the estimation of these parameters is of interest beyond simply determining the evolutionary history of a group of species. Second, stochastic models can correct for multiple substitutions that occur along the branches of a phylogeny. Multiple substitutions can make analysis of genes with high substitution rates, or of groups that diverged a long time ago, problematic. Finally, Poisson process models can be compared directly and the assumptions of the analysis potentially improved (Goldman 1993). This is not done easily using methods that do not precisely specify their assumptions.

The stochastic models that are used in phylogenetic analysis are all Markov chain models. For a Markov chain, the state of the process in the next interval of time only depends on the current state. Moreover, the models that are currently used assume that the number of substitutions on the phylogenetic tree follows the Poisson distribution; hence, these types of models are called Poisson process models. At the heart of any Poisson process model of substitution is a matrix that specifies the instantaneous rate of change from one state to another. The simplest model assumes that the rates of change among all nucleotides are equal and that the frequencies of the nucleotides in the sequence are equal (Jukes and Cantor 1969) (Fig. 5.3.4.1). Once the rates of change among different nucleotides have been specified, the probability of a change from one nucleotide to another over evolutionary time can be calculated. For the Jukes–Cantor model, these probabilities are

$$p_{ij}(v) = \begin{cases} \frac{1}{4} + \frac{3}{4}e^{-\frac{4}{3}v}, & i = j \\ \frac{1}{4} - \frac{1}{4}e^{-\frac{4}{3}v}, & i \neq j \end{cases} \quad (1)$$

where $p_{ij}(v)$ is the probability of a change from nucleotide i to nucleotide j over a branch of length v. The length of the branch is in terms of expected number of substitutions per site, and is the product of substitution rate and time. Figure 5.3.4.2 illustrates the relationship between the length of the branch and the probability of observing a change along the branch for the Jukes–Cantor model. When the length of the branch $v=0$, then the two sequences must be identical. As the length of the branch becomes longer, the expected proportion of sites that differ increases.

Models of DNA substitution have been modified extensively to reflect biology more closely. For example, the rate matrix describing how nucleotides change in an instant of time has been made more general to relax the assumption that all substitution types occur at the same rate. The most general model commonly used is called the General Time Reversible (GTR) model. Other models are special cases of the GTR model. Figure 5.3.4.1 shows several examples of substitution models commonly used in phylogenetic analyses. The models have been modified to accommodate differences in the frequencies

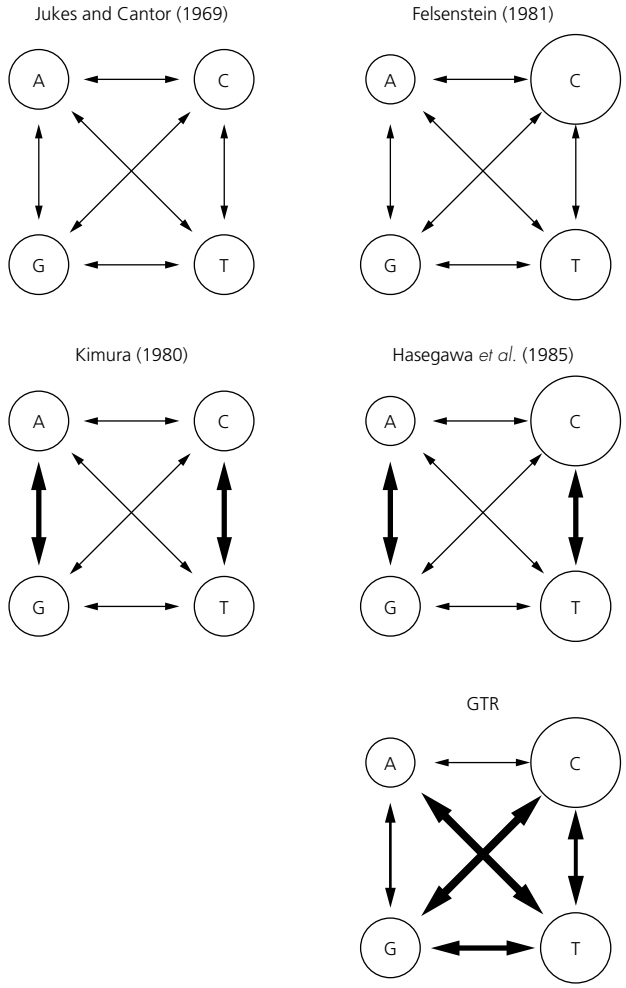

Fig. 5.3.4.1 Some examples of commonly used Poisson process models of DNA substitution. The size of the circles surrounding each nucleotide is proportional to the stationary frequency of the base whereas the thickness of the arrows between bases represents the relative rates of substitution among the different nucleotides. The Jukes–Cantor (1969) model of DNA substitution assumes that the stationary frequency and substitution rates among nucleotides are equal. The Felsenstein (1981) model relaxes the constraint that the bases have equal frequencies, whereas the Kimura (1980) model relaxes the constraint that all substitution types have equal rates by allowing transitions to occur at a different rate than transversions. The model proposed by Hasegawa *et al.* (1985) relaxes both assumptions simultaneously. The General Time Reversible (GTR) model is the most general four-state model commonly used in phylogenetics; it allows all the nucleotides to have different stationary frequencies and also allows each substitution type a unique rate.

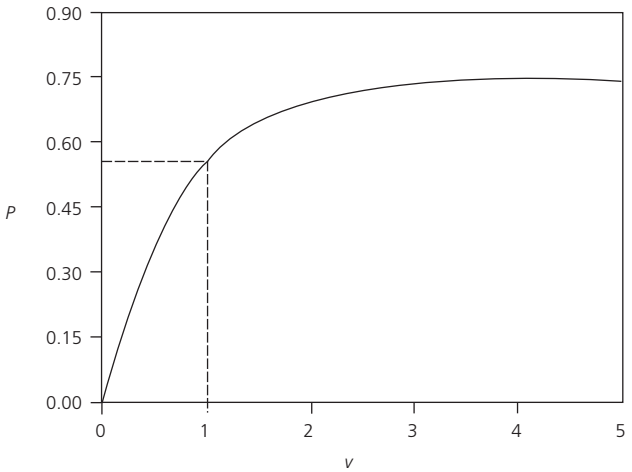

Fig. 5.3.4.2 The relationship between the length of the branch separating two sequences (v) and the proportion of sites expected to be different (P) under the Jukes–Cantor (1969) model of DNA substitution. If the proportion of sites that differs between two sequences (P) is known, then a distance between the two sequences (v) can be obtained. This distance is corrected for superimposed substitution events that obscure the true number of changes that separates the two sequences.

of different nucleotides (the size of the circles surrounding the base in the figure) as well as differences in the rates of change among nucleotides (the size of the arrows between nucleotides). For example, the Kimura (1980) model and the model proposed by Hasegawa *et al.* (1985) allow transitions to occur at a higher rate than transversions. The only difference between the two models is that Kimura's constrains the nucleotide frequencies to be equal whereas that of Hasegawa *et al.* does not. More interestingly, the substitution models have been modified to accommodate limited dependence among sites. For example, compensatory substitutions in the stem regions of ribosomal genes, and within codons of protein-coding genes, can now be accommodated (e.g. Goldman and Yang 1994; Schöniger and von Haeseler 1994).

It is clear that different sites have different rates of substitution (probably because different sites in a DNA sequence are more or less constrained by selection). Several different approaches have been taken to relax the assumption in a phylogenetic analysis that all sites evolve at the same rate. One approach assumes that the rate at a site is unknown, but drawn from a distribution such as the gamma distribution (e.g. Jin and Nei 1990). Another approach has been to assign different sites to classes, such as first, second, and third codon positions, and then estimate the rate for each class separately. Both approaches usually provide significant improvements in the fit of the model to the observed sequences.

The same approaches used to model the substitution process in nucleotides can be applied to amino acid sequences (Adachi and Hasegawa 1992). Here, however, instead of four different states (the nucleotides A, C, G, and T), there are 20 possible states (for the 20 different amino acids). One challenge has been to modify the substitution model in such a way that a good fit to amino acid sequences is obtained without too many parameters.

Distance methods on the one hand, and maximum likelihood and Bayesian methods on the other, use models of DNA substitution in different ways. Distance methods use a model of DNA substitution to correct for multiple substitutions when constructing a matrix of pairwise comparisons of sequences. For example, the simplest Poisson process model used in analysis of DNA sequences is the model proposed by Jukes and Cantor (1969). The transition probabilities of the Jukes–Cantor model were given above. The distance between two sequences as predicted by the Jukes–Cantor model of DNA substitution is:

$$v = -\tfrac{3}{4}\ln(1-\tfrac{4}{3}P) \qquad (2)$$

where P is the observed proportion of different nucleotides between the two sequences and v is the estimate of the number of substitutions per site that separates the two sequences. Figure 5.3.4.2 shows the relationship between the length of the branch, v, and the expected proportion of sites that differ between the two sequences, P. The dashed line illustrates that if the proportion of sites that differ between the two sequences is known, then the number of substitutions separating the two sequences can be back-calculated. In general, the number of substitutions separating two sequences will be the proportion of sites that differ between the two sequences plus some additional number of substitutions that changed multiple times in the history of the species. Jukes–Cantor distances will accurately correct for multiple substitutions when the evolutionary process obeys very simple rules (such as equal rates across sites and equal rates of substitution among nucleotides). When the assumptions of the model are violated, as they undoubtedly are with observed DNA sequences, the correction for multiple substitutions may be biased. However, the distances between sequences may also be calculated using more complicated models of substitution.

Maximum likelihood and Bayesian methods use models of DNA substitution to calculate the probability of observing the aligned sequences given the model. At some point, both methods calculate

$$\Pr[\text{Aligned Sequences} \mid \text{Tree and Nuisance Parameters}] \qquad (3)$$

Here, the vertical line '|' is read 'given', and the above represents the probability of observing the full dataset given a specific tree and specified other parameters. The

other (nuisance) parameters might include the lengths of the branches on the phylogenetic tree as well as parameters of the substitution model (such as the relative rate of transitions vs. transversions). This probability is calculated as the product of the probability for observing each site and is a sum over all possible assignments of nucleotides to the internal nodes of the phylogenetic tree. For even moderately large datasets, this probability can become very small; to facilitate keeping the probability accurately in computer memory, the log of the probability is typically used.

Estimating phylogeny

Maximum parsimony

The best tree under the parsimony criterion is the tree that minimizes the number of character changes. Assuming that each character transition has equal weight, the minimum number of character-state transitions on a tree can be calculated using an algorithm first proposed by Fitch (1971).

Distance methods

Distance methods estimate phylogeny in a two-step procedure. First, a matrix of pairwise distances among sequences is constructed. The distances are in terms of the expected number of substitutions per site that separate the sequences. The distance matrix is treated as the observed data and used to construct a phylogeny. Several different criteria can be used to estimate phylogeny given a distance matrix. These include least squares (e.g. Cavalli-Sforza and Edwards 1967) and minimum evolution (Rzhetsky and Nei 1992; the neighbour joining method is thought of as a stepwise addition algorithm for finding minimum evolution trees, Saitou and Nei 1987; Swofford *et al.* 1996). The basic idea for both of these methods is to minimize the conflict between a tree (with branch lengths specified) and the data.

Maximum likelihood

Maximum likelihood takes the tree that maximizes the probability of observing the data as the best estimate of phylogeny, i.e. the tree that maximizes the likelihood function

$$\text{Like(Tree)} = c\ \Pr[\text{Data} \mid \text{Tree and Nuisance Parameters}] \tag{4}$$

where Like(Tree) is the likelihood for the specific tree and c is a constant that can take any value (and is typically set to 1). The tree that maximizes this probability is called the maximum likelihood estimate of phylogeny. Typically, the likelihood is also maximized with respect to the nuisance parameters. That is, even though the systematist is not interested in any parameters of the model except the tree relating the species, maximum likelihood values of the nuisance parameters are obtained in the course of the analysis. The maximum likelihood method was formalized in statistics by R.A. Fisher, and its application to phylogenetics developed by Edwards and Cavalli-Sforza (1964) and Felsenstein (1981).

Bayesian inference

The object of Bayesian inference is the posterior probability of a parameter. Whereas the maximum likelihood estimate of phylogeny is the tree that maximized

$$\Pr[\text{Data} \mid \text{Tree and Nuisance Parameters}] \tag{5}$$

Bayesians concentrate their attention on

$$\Pr[\text{Tree} \mid \text{Data}] \tag{6}$$

which is called the posterior probability of the phylogeny given the aligned sequences. The tree with the greatest probability is usually taken as the best estimate of phylogeny. The posterior probability of the phylogeny can be calculated using Bayes formula

$$\Pr[\text{Tree} \mid \text{Data}] = \frac{\Pr[\text{Data} \mid \text{Tree}] \times \Pr[\text{Tree}]}{\Pr[\text{Data}]} \tag{7}$$

Note that the probabilities do not depend upon the specific values of the nuisance parameters; the nuisance parameters have been eliminated by integrating the posterior probability over all possible values for the nuisance parameters. The term Pr[Tree] is the prior probability of the phylogeny. The prior probability may be difficult to specify and represents the systematist's knowledge about the phylogeny before any data have been observed. Two different approaches have been taken to specify the prior probability of a tree. A 'biological' prior lets the birth–death process of cladogenesis specify the probability of a tree and branch lengths on it (Rannala and Yang 1996). An 'uninformative' prior, on the other hand, treats all topologies as equally probable before any data have been observed (Newton *et al.* 1997). Moreover, the lengths of the branches are drawn from a uniform distribution.

The probability in the denominator of equation (7) involves, minimally, a summation over all possible trees and a multidimensional integral over the different branch lengths for a given tree. For five or six species, the denominator can be evaluated using widely available numerical methods (Rannala and Yang 1996). However, for more than six species, it is necessary to evaluate the posterior probability using more exotic methods, such as Markov chain Monte Carlo.

Once the posterior probabilities of different trees are in

hand, the Bayesian can make inferences about the parameter(s) of interest. For the phylogeny problem, it is typical to take the tree with the greatest posterior probability as the best estimate of phylogeny (Rannala and Yang 1996).

Assessing confidence

Once a systematist has a tree in hand, how can its reliability be inferred? In what is widely considered a contentious field, this question ranks among the most debated. Many different methods have been proposed. These include evaluating indices associated with a tree, evaluating the number of steps it takes to destroy a clade (Bremer decay index; Bremer 1988), various permutation approaches, and resampling methods (e.g. the bootstrap and the jackknife).

For standard statistical problems, confidence intervals can be erected around a parameter estimate in a straightforward manner. For example, suppose n observations $x_1, x_2, \ldots, x_n$ are drawn from a normal distribution [$N(\mu, \sigma)$] with unknown mean (μ) and known variance ($\sigma=1$). A maximum likelihood or method of moments estimate of the mean (μ) is $\bar{x}$ (the arithmetic mean). A 95% confidence interval can be constructed around this estimate by taking advantage of the fact that the probability distribution of $\bar{x}$ is normal with mean μ and variance σ^2/n [$N(\mu, \sigma^2/n)$].

$$\Pr\left[\bar{x} - \frac{1.96}{\sqrt{n}} < \mu < \bar{x} + \frac{1.96}{\sqrt{n}}\right] = 0.95 \tag{8}$$

The interpretation of this confidence interval is that if the experiment were repeated many times, drawing n observations from the same distribution over and over, in 95% of the cases the true value of the mean of the distribution (μ) would fall in the confidence interval.

Note that in order to construct the confidence interval, the sampling distribution of $\bar{x}$ must be known [in the above case, $N(\mu, \sigma^2/n)$]. However, for many statistical problems, the sampling distribution is unknown, or very difficult to obtain or calculate. In these cases, the observed data can substitute for the unknown distribution. That is, instead of going through the thought experiment of drawing from a known distribution, b samples are drawn from the observed distribution (data). For each of the replicates, the parameter is estimated again resulting in b estimates ($\theta_1, \theta_2, \ldots, \theta_b$). These estimates can be used to construct a confidence interval around the original estimate (θ).

Both the bootstrap and the jackknife have been used in phylogenetics (see Felsenstein 1985; Penny and Hendy 1985). For the bootstrap, b replicate datasets are constructed by sampling sites at random, and with replacement from the original dataset, to construct new datasets of the same size as the original. For the jackknife, b replicate datasets are constructed by randomly deleting c sites from the original dataset (such that 36% or 50% or some other fraction of the sites are deleted). For each replicate dataset, the phylogeny is estimated, resulting in b estimates of phylogeny. This 'cloud' of trees in some sense represents a confidence interval around the original estimate of phylogeny. However, the exact interpretation of this 'cloud' remains uncertain. The typical approach is to summarize the clades that are in common among these trees using majority rule consensus (Felsenstein 1985). If a clade is found in a high proportion of the replicates, then more confidence can be placed in the estimate.

Bayesian phylogeny estimation suggests another way of assessing the confidence that can be placed in a tree. The end result of a Bayesian analysis is a probability that is assigned to each possible phylogenetic tree. The probability that a certain clade (say a clade that has taxa A, B, and C monophyletic) is real is simply the sum of the probabilities of the trees that have A, B, and C monophyletic (Larget and Simon 1999). The easy interpretation of posterior probabilities may be one of the main advantages of the Bayesian approach to phylogenetic inference.

Testing models of DNA substitution

As noted above, all phylogenetic methods make specific assumptions about the evolutionary process. Importantly, the quality of a phylogenetic analysis may depend critically upon the accuracy of these assumptions. Simulation studies, for example, show that failure to accommodate among-site rate variation can lead to erroneous results in a phylogenetic analysis of DNA sequences. How can the assumptions of an analysis be tested and the model improved?

One commonly used method for testing the fit of a model of DNA substitution involves using likelihood. Likelihood provides a direct means for comparing hypotheses on the same dataset. That is, if one hypothesis makes observing the data more probable, then that hypothesis should be favoured. The hypotheses can be compared through the ratio of their likelihoods:

$$\frac{\Pr[\text{Data} \mid \text{Hypothesis 1}]}{\Pr[\text{Data} \mid \text{Hypothesis 2}]} \tag{9}$$

If Hypothesis 1 makes observing the data more probable than Hypothesis 2, then that hypothesis is favoured. Similarly, if the probability of observing the data is greater under Hypothesis 2, then that hypothesis is favoured. Typically, the maximum probability of observing the data under each hypothesis is calculated:

$$\Lambda = \frac{\max(\Pr[\text{Data} \mid \text{Hypothesis 1}])}{\max(\Pr[\text{Data} \mid \text{Hypothesis 2}])} \tag{10}$$

For the special case in which Hypothesis 1 (the null hypothesis) is a special case of Hypothesis 2 (the alternative hypothesis), Λ will always be less than 1 and the significance of the improvement in the likelihood afforded by the alternative hypothesis can be approximated by comparing $-2\log_e\Lambda$ to a χ^2 distribution with q degrees of freedom. The degrees of freedom for the test is the difference in the number of free parameters between the alternative and null hypotheses.

Many hypotheses in phylogenetics are nested and likelihood ratio testing can be performed using the χ^2 approximation. There are currently likelihood ratio tests available to examine the molecular clock (Felsenstein 1981) and to compare the fit of models of DNA substitution to observed sequences (Goldman 1993). For cases in which the null and alternative hypotheses are not nested, the significance of the likelihood ratio test statistic (Λ) can be calculated using simulation (Goldman 1993). Simulation has been used to test the adequacy of models of DNA substitution (Goldman 1993) and to examine agreement among trees (see Huelsenbeck and Rannala 1997). Although less work has been done on hypothesis testing using distance methods, tests of the fit of models of DNA substitution that are appropriate for distance data have also been developed (e.g. see Rzhetsky and Nei 1995).

Conclusions

Molecular phylogenetics has changed the way biologists approach many questions in evolutionary biology. It is also changing how biologists approach questions that could traditionally be addressed only by palaeontologists (e.g. estimating speciation and extinction rates and the times of divergence of clades). Many of the advances have come through improvements in the models of DNA substitution assumed by phylogenetic methods, and through the introduction of new algorithms (such as Markov chain Monte Carlo). Bayesian and maximum likelihood estimations of phylogeny, for example, have the potential to allow biologists to ask still more complex questions using molecular data.

References

Adachi, J. and Hasegawa, M. (1992) Amino acid substitution of proteins coded for in mitochondrial DNA during mammalian evolution. *Japanese Journal of Genetics* **67**, 187–197.

Bremer, K. (1988) The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* **42**, 795–803.

Cavalli-Sforza, L.L. and Edwards, A.W.F. (1967) Phylogenetic analysis: models and estimation procedures. *American Journal of Human Genetics* **19**, 233–257.

Edwards, A.W.F. and Cavalli-Sforza, L.L. (1964) Reconstruction of evolutionary trees. In: J. McNeill, ed. *Phenetic and phylogenetic classification*, pp. 67–76. Systematics Association Publication, London.

Felsenstein, J. (1981) Evolutionary trees from DNA sequences: a maximum likelihood approach. *Journal of Molecular Evolution* **17**, 368–376.

Felsenstein, J. (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39**, 783–791.

Fitch, W.M. (1971) Toward defining the course of evolution: minimal change for a specific tree topology. *Systematic Zoology* **20**, 406–416.

Goldman, N. (1993) Statistical tests of models of DNA substitution. *Journal of Molecular Evolution* **36**, 182–198.

Goldman, N. and Yang, Z. (1994) A codon-based model of nucleotide substitution for protein-coding DNA sequences. *Molecular Biology and Evolution* **11**, 725–736.

Hasegawa, M., Kishino, K. and Yano, T. (1985) Dating the human–ape splitting by a molecular clock of mitochondrial DNA. *Journal of Molecular Evolution* **22**, 160–174.

Huelsenbeck, J.P. and Rannala, B. (1997) Phylogenetic methods come of age: testing hypotheses in an evolutionary context. *Science* **276**, 227–232.

Jin, L. and Nei, M. (1990) Limitations of the evolutionary parsimony method of phylogenetic inference. *Molecular Biology and Evolution* **7**, 82–102.

Jukes, T.H. and Cantor, C.R. (1969) Evolution of protein molecules. In: H.M. Munro, ed. *Mammalian protein metabolism*, pp. 21–132. Academic Press, New York.

Kimura, M. (1980) A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* **16**, 111–120.

Larget, B. and Simon, D.L. (1999) Markov chain Monte Carlo algorithms for the Bayesian analysis of phylogenetic trees. *Molecular Biology and Evolution* **16**, 750–759.

Newton, M., Mau, B. and Larget, B. (1997) Markov chain Monte Carlo for the Bayesian analysis of evolutionary trees from aligned molecular sequences. In: *Proceedings of the AMS-IMS-SIAM Joint Summer Research Conference on Statistics and Molecular Biology.*

Penny, D. and Hendy, M.D. (1985) Testing methods of evolutionary tree construction. *Cladistics* **1**, 266–278.

Rannala, B. and Yang, Z. (1996) Probability distribution of molecular evolutionary trees: a new method of phylogenetic inference. *Journal of Molecular Evolution* **43**, 304–311.

Rzhetsky, A. and Nei, M. (1992) A simple method for estimating and testing minimum-evolution trees. *Molecular Biology and Evolution* **9**, 945–967.

Rzhetsky, A. and Nei, M. (1995) Tests of applicability of several substitution models for DNA sequence data. *Molecular Biology and Evolution* **12**, 131–151.

Saitou, N. and Nei, M. (1987) The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Molecular Biology and Evolution* **4**, 406–425.

Schöniger, M. and von Haeseler, A. (1994) A stochastic model for the evolution of autocorrelated DNA sequences. *Molecular Phylogenetics and Evolution* **3**, 240–247.

Swofford, D.L., Olsen, G.J., Waddell, P.J. and Hillis, D.M. (1996) Phylogenetic inference. In: D.M. Hillis, C. Moritz and B.K. Mable, eds. *Molecular systematics*, 2nd edn, pp. 407–514. Sinauer Associates, Sunderland, Massachusetts.

Wheeler, W.C. and Gladstein, D. (1994) *MALIGN* (Version 1.89). American Museum of Natural History, New York.

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5.3.5 Molecules and Morphology in Phylogeny—the Radiation of Rodents

F.M. CATZEFLIS

Introduction

Molecular and morphological phylogenies should reveal the same unique evolutionary history of organisms, provided that the characters upon which they are based are not excessively homoplasic. Rodents (Rodentia: Mammalia) provide an excellent example of conflict between inferences from molecular and morphological data in evolutionary systematics. The fossil record of rodents is exceptionally abundant, and shows that this taxon was speciose from its origin (Hartenberger 1998). Most Palaeogene remains of rodents are teeth; hence systematists have relied heavily upon dental characters for integrating extinct and living taxa in phylogenies, while recognizing that much homoplasy is present in these structures (Luckett and Hartenberger 1993). Molecular systematics of rodents is a relatively new field, but there are some studies based on a large enough taxonomic sample to test morphological hypotheses (Nedbal *et al.* 1996; Huchon *et al.* 1999).

The phylogeny of rodents is still far from settled, and the major controversies include:

1 The very nature of the taxon Rodentia—is it monophyletic? The rodents appear to be united by a number of morphological synapomorphies (Luckett and Hartenberger 1993), but complete mitochondrial DNA sequences for a few representatives suggest that Rodentia is paraphyletic (Reyes *et al.* 1998).

2 The identity of the sister-taxon of rodents—is it Lagomorpha (rabbits, pikas, and their relatives)? That is, does Glires (Rodentia+Lagomorpha) form a natural supraordinal clade?

3 How many major (suprafamilial) taxa belong within the rodents, and what are their relationships (see Nedbal *et al.* 1996)? Are Muroidea (e.g. rats, mice, voles, gerbils, hamsters) and Dipodoidea (jerboas, jumping-mice) related? Does Sciurognathi (all non-hystricognath rodents) represent a clade? Are Old-World and New-World porcupines two independent expressions of the same 'Bauplan', which arose independently and evolved a convergent morphology?

Diversity

Morphologists and molecularists recognize that rodents exhibit a tremendous biodiversity; both living and extinct rodents are represented by high numbers of taxa at various hierarchical levels, from species to super-family. Fifty-two families are recognized from Lower Eocene to Middle Miocene time (Fig. 5.3.5.1), of which 29 are still extant (Hartenberger 1998). Analysis of the fossil record through time and space suggests that an impressive *radiation* occurred; 10 families appeared in the Lower Eocene, increasing to a diversity of 21 during the Middle Eocene.

The real challenge for molecular phylogeneticists is to encompass this diversity, rather than reducing rodents to just mouse, rat, and guinea-pig (see references in Luckett and Hartenberger 1993; Nedbal *et al.* 1996; Reyes *et al.* 1998). Rodents represent 44% of all 4629 species of living mammals, and 28% of the 160 recognized families. Higher-level phylogenetic hypotheses cannot be tested satisfactorily without considering representatives of at least 8–12 major lineages: Muroidea, Gliroidea (dormice, graphiures), Geomyoidea (pocket gophers, kangaroo-rats), Sciuroidea (squirrels, marmots, mountain-beavers), Anomaluromorpha (scaily tailed flying squirrels, springhares), Castoroidea (beavers), Dipodoidea (jerboas, jumping-mice), Ctenodactyloidea (gundis), Phiomorpha (cane-rats, mole-rats, rock-rats, Old-World porcupines), and Caviomorpha (guinea-pigs, chinchillas, degus, casiraguas, coypu, New-World porcupines). As most families of rodents are of relatively ancient origin (compared to other eutherian mammals), robust and reliable molecular inferences can only be drawn with a taxonomic sampling of two or three representative examples of these major lineages.

Molecular systematics

The molecular systematics of the various families and superfamilies of rodents is still being researched. The most appropriate genetic markers for these fast-evolving mammals are slow-evolving, single-copy nuclear genes, and there are presently too few data to test the radiation hypothesis (see references in Huchon *et al.* 1999). Initial investigations based on amino-acid sequences (haemoglobins; pancreatic ribonucleases) have considered the taxonomic diversity of rodents in a limited way, and reached a few conclusions in general agreement with traditional systematics.

Nucleotide sequences of two mitochondrial genes (protein-coding cytochrome *b* and ribosomal 12S RNA) are available for at least one representative example of 10 major rodent lineages (see above), as well as for several other eutherian and a couple of marsupial orders (represented by *Macropus* and *Didelphis*). An analysis of both these genes, combined in tandem for 24 rodent genera (representing 17 families), supports a large basal polytomy leading to eight groups (Fig. 5.3.5.2), a solution which is at least consistent with a true radiation. A cluster of interest is the one uniting squirrels, mountain-

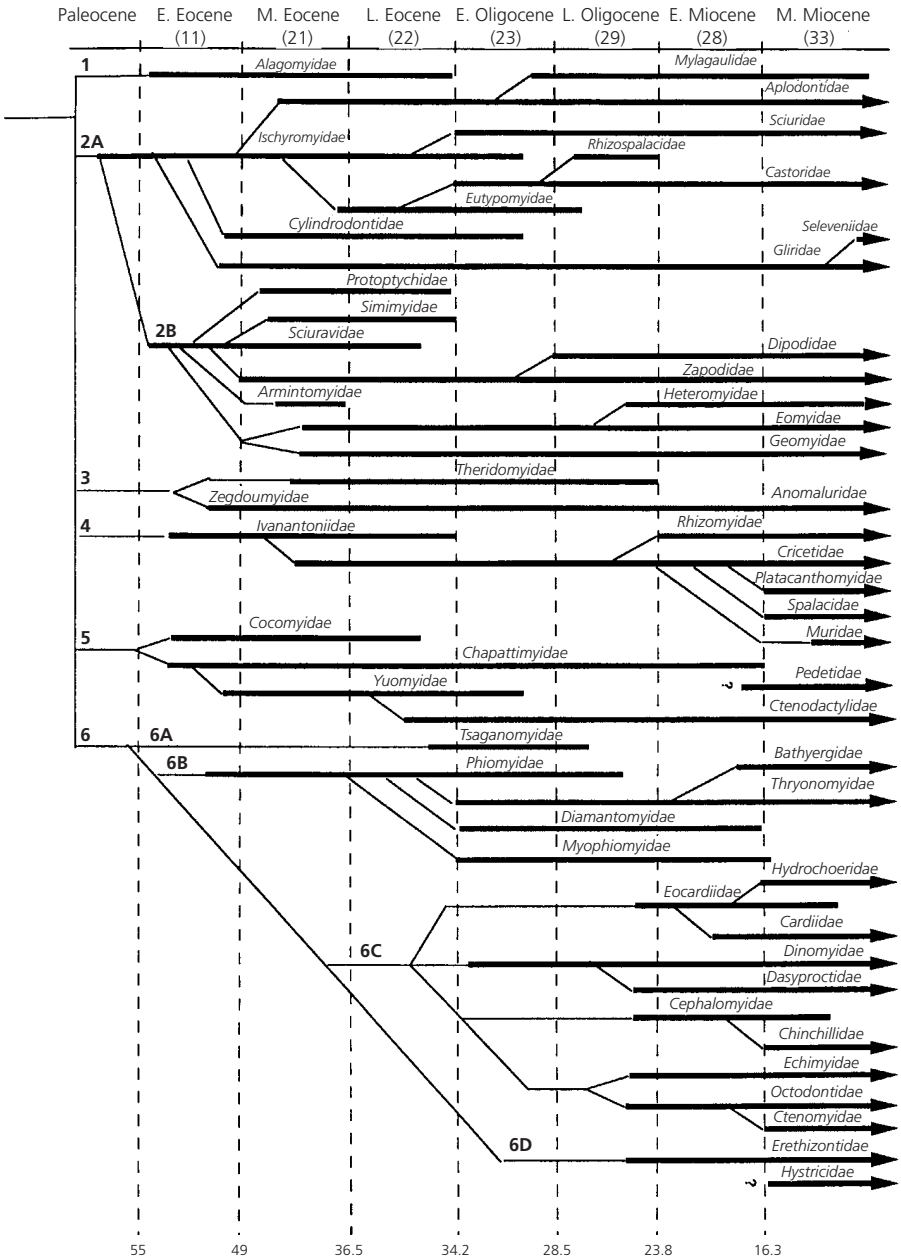

Fig. 5.3.5.1 Geological time scale and fossil record of the 52 recognized families of rodents, from the Paleocene to the Middle Miocene (values in parentheses indicate the numbers of families for each geological stage). Thin lines connecting taxa indicate possible relationships, although many of them are still in dispute. The numbers 1–6 along ancestral segments denote infraordinal and subordinal taxa proposed by Hartenberger (1998): 1, 2A, 2B, unnamed; 3, Parasciurognatha; 4, Murida; 5, Ctenodactylomorpha; 6, Hystricognatha (A, Tsaganomyidae; B, Phiomorpha; C, Caviida; D, Erethizontidae). Values along the bottom are radiometric ages expressed in Ma. (From Hartenberger 1998.)

beavers, and dormice (Sciuridae, Aplodontidae, and Gliridae) because it identifies a probable subclade among sciurognaths, which has never been convincingly shown to be monophyletic. When representative examples of non-rodent eutherian orders are included in the data matrix, no support for the monophyly of rodents is evident, but neither is there a robust signal for a paraphyletic Rodentia (data not shown). Caution is necessary when interpreting this branching pattern because there is evidence for saturation (parsimony-inferred changes more numerous than changes observed in the data matrix) in several parts of both genes, which may evolve too rapidly for this level of analysis.

Nuclear markers may be more appropriate than fast-evolving mitochondrial genes for deciphering such ancient and numerous cladogenetic events. An analysis based on 1200 protein-coding nucleotides of von Willebrand factor gene for 15 rodent and three lagomorph species also suggested a large multitomy for the simultaneous emergence of Dipodoidea, Muroidea, Hystricognathi (New-World caviomorphs and Old-World phiomorphs), Gliridae, and Sciuroidea. Investigations based on improved taxonomic sampling and on other nuclear genes (e.g. interphotoreceptor retinoid-binding protein, C-myc proto-oncogene) should shed more light on the phylogeny of Rodentia.

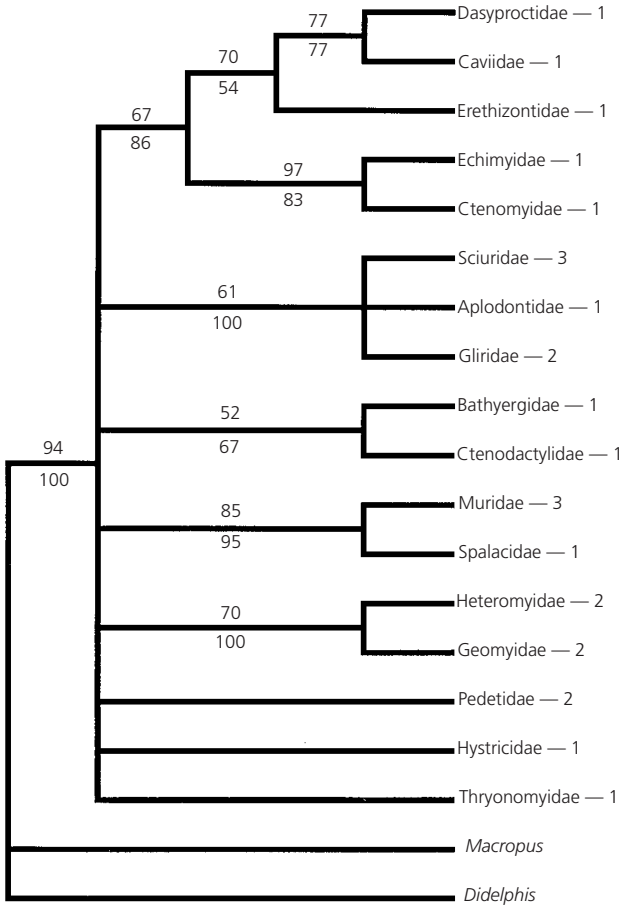

Fig. 5.3.5.2 Molecular phylogenetic tree for 25 rodent species representing 17 families. This branching pattern is a majority-rule consensus tree after 1000 bootstrap replications of a maximum parsimony analysis for 1963 sites-characters representing the least variable changes for both mitochondrial 12S rRNA (823 sites) and cytochrome *b* (1140 sites) genes. Values along ancestral segments are percentage reliability for a maximum likelihood analysis (above) and bootstrap percentages for a maximum parsimony analysis (below). Numbers after each family indicate how many representative species were involved. The tree was rooted by the two marsupial sequences (*Macropus*, *Didelphis*). (Unpublished data, Institut des Sciences de l'Evolution, Université Montpellier, June 1999.)

The molecular clock

A by-product of comparative molecular analysis of particular interest to palaeobiologists is the application of the 'molecular clock' to the dating of cladogenetic events. Much controversy has centred around the rate of DNA change in some rodents compared with other eutherians. Studies of nuclear genes have suggested that murid (mice, rats) and cricetid (hamsters, voles) Muroidea were evolving much faster than hominid primates, but this is disputed by other works. A synthesis (Kumar and Hedges 1998), making use of numerous nuclear genes, emphasized the discrepancy between molecular and palaeontological estimates for several events in the phylogeny of rodents: the *Mus*/*Rattus* (mouse/rat) dichotomy is dated 41 Ma (molecular) vs. 12–14 Ma (palaeontological); Murinae/Cricetinae (mice/hamsters) is dated 66 Ma vs. 20–25 Ma; and Gerbillinae/Murinae (gerbils/mice) 66 Ma vs. 18–25 Ma. These differences await a widely accepted explanation. More sophisticated analytical methods are required to handle the heterogeneities in substitution rate between and among both genes and taxa. It is possible that the nuclear genome of most muroid rodents evolves particularly fast. Nevertheless, other studies have revealed a rather heterogeneous rate of DNA change among and between some families of rodents (Huchon *et al.* 1999): Sciuroidea (squirrels, marmots, mountain-beaver) appear slow-evolving in comparison with several Caviomorpha (guinea-pigs, agoutis).

Conclusion

A comparison of morphological and molecular phylogenetic trees (Figs 5.3.5.1 and 5.3.5.2) reveals that much remains to be done to diminish the conflict between morphology and molecules. Molecular phylogenetics should consider additional slow-evolving genes with an improved taxonomic sampling. Such data might, in the future, reconcile both approaches, and allow the controversies raised in the introduction to be addressed.

References

Hartenberger, J.-L. (1998) Description de la radiation des Rodentia (Mammalia) du Paléocène supérieur au Miocène: incidences phylogénétiques. *Comptes Rendus de l'Académie Sciences Paris* **326**, 439–444.

Huchon, D., Catzeflis, F.M. and Douzery, E.J.P. (1999) Molecular evolution of the nuclear von Willebrand Factor gene in mammals and the phylogeny of rodents. *Molecular Biology and Evolution* **16**, 577–589.

Kumar, S. and Hedges, S.B. (1998) A molecular timescale for vertebrate evolution. *Nature* **392**, 917–920.

Luckett, W.P. and Hartenberger, J.-L. (1993) Monophyly or polyphyly of the order Rodentia: possible conflict between morphological and molecular interpretations. *Journal of Mammalian Evolution* **1**, 127–147.

Nedbal, M.A., Honeycutt, R.L. and Schlitter, D.A. (1996) Higher level systematics of rodents (Mammalia, Rodentia): evidence from the mitochondrial 12S gene. *Journal of Mammalian Evolution* **3**, 201–237.

Reyes, A., Pesole, G. and Saccone, C. (1998) Complete mitochondrial DNA sequence of the fat dormouse, *Glis glis*: further evidence of rodent paraphyly. *Molecular Biology and Evolution* **15**, 499–505.

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5.3.6 Using Molecular Data to Estimate Divergence Times

A. COOPER, N. GRASSLY and A. RAMBAUT

Introduction

The use of molecular data to estimate the timing of biological events in the past has provided an important new opportunity to both augment and, perhaps more importantly, complement the palaeontological record. While many molecular studies have supported classical hypotheses gleaned from the fossil record, there have also been surprising conflicts, particularly about the origins of major taxonomic groups where molecular data often suggests much earlier dates than the fossil record (Cooper and Fortey 1998). Molecular dating techniques utilize the fact that genomes accumulate mutations over time and that the genetic distance between two taxa will therefore be proportional to the time since they last shared a common ancestor. By calibrating measures of the genetic divergence between taxa with palaeontological or biogeographical events, a rate of evolution can be calculated and then applied to other taxa where such data are lacking. Unfortunately, several sources of variability inherent in molecular date estimates are commonly overlooked, particularly errors in modelling the substitution process, and the results of many studies have been presented with unrealistically narrow confidence limits. Recent advances using likelihood-based approaches have produced more realistic, but larger, confidence intervals. Consequently, until the availability of long molecular sequences improves, molecular dates are best used to test specific hypotheses of divergence dates, such as those suggested by evolutionary transitions at major geological boundaries.

Molecular dates have been obtained from a variety of protein and DNA–DNA hybridization data, but the majority of studies have used nucleotide sequences. The molecular dating of recent events within populations, or of lineages which hybridize or recombine, presents special problems which are beyond the scope of this review. Above the species level, matters are simplified since intrapopulation variation becomes small in relation to the genetic distances between species, and gene trees (the phylogenetic history indicated by a gene within an individual) converge towards species trees (the phylogenetic history of a species). Molecular dating studies focus on data from basic 'housekeeping' genes, which are unlikely to be strongly influenced by morphological evolution, so that rapid radiations (e.g. during the Early Cambrian and Tertiary) do not cause rates of molecular evolution to accelerate (Cooper and Fortey 1998).

General problems

Molecular dating techniques include several steps which can be subject to error, including modelling the substitution process, estimating the amount of molecular change between taxa since divergence, and calibrating the evolutionary rate. Models of the molecular clock typically assume that the numbers of substitutions over time in a nucleotide sequence can be approximated by a Poisson distribution, which is reasonable if the expected number of substitutions at each site over the observed time period is small. However, even if the molecules evolve according to this model, and the genetic distances and calibrations are assumed to be known without error, the confidence intervals on divergence dates are quite large due to the stochastic nature of the substitution process (Table 5.3.6.1). Further variance in date estimates can occur because of failures of a model to deal with differences in the rates of change between nucleotides at a given sequence position (e.g. transversion/transition bias, where one form of sequence substitution is more common than another), or in the rate or pattern of substitution along the sequence.

Estimates of genetic distance are influenced by the number of substitutions observed, variation in the molecular clock 'tick-rate', and the accuracy of phylogenetic reconstruction methods. Confidence intervals narrow as the number of observed substitutions between taxa increases, although if the rates of substitution are too high then multiple changes at a single sequence position cause saturation problems, where the total number of substitutions is underestimated. Differences in the 'tick-rate', or speed, at which mutations arise happen because the number of substitutions occurring on a branch in a given amount of time can vary due to the stochastic nature of the substitution process or, more problematically, through systematic variation between lineages. Such rate heterogeneity has been correlated with the generation time, body size, or metabolic rate of taxa amongst other factors, and needs to be considered in all clock studies.

Calibrating the genetic distance with a palaeontological or biogeographical date produces an evolutionary rate—an estimate of molecular change per unit time which can then be applied to other taxa. Generally, the rate is regarded as a maximum estimate because the calibration point is often the lower limit of a possible range (e.g. the earliest fossil occurrence of a taxon which may have originated some time previously), and errors associated with saturation are biased towards the underestimation of large genetic distances. The rate must be tested first to determine its applicability to different parts of the tree. A common method is to test for rate constancy by using multiple pairwise genetic distance comparisons and more than one calibration date. However, this may produce overly confident

Table 5.3.6.1 The range of 95% confidence intervals for a simple likelihood model where substitutions are expected to follow a Poisson distribution, and the fossil calibration and genetic distances are assumed to be known without error. The confidence intervals are expressed as a percentage of the estimated divergence date, for differing numbers of substitutions separating a pair of calibration taxa and a pair whose divergence date is to be estimated. As an example, studies of nuclear and mitochondrial nucleotide sequences from the modern bird orders surprisingly indicated that they diverged well before the Cretaceous–Tertiary boundary (Cooper and Fortey 1998). If the divergence of the ratite rhea and ostrich (57 substitutions) is calibrated with a mid-Paleocene (60 Ma) rhea fossil, then the calibrated rate is 0.95 subs/myr. The ratite pair are separated from the loon and shearwater by 98 substitutions, so the estimated divergence date of the two pairs is 103 Ma, while the Poisson distribution gives a confidence interval of 74–145 Ma (the table gives an approximate figure of 71.6–141.4 Ma). It is important to note that the table only gives the ranges associated with a Poisson distributed substitution process, and that these would increase when other sources of error (e.g. genetic distance and calibration) are included.

Substitutions in calibration	Observed substitutions in genetic divergence to be dated				
	5	10	50	100	500
5	27.8–359.6	35.3–321.0	44.0–287.7	45.2–283.3	46.3–279.8
10	31.2–281.4	41.0–243.7	53.0–209.2	55.0–204.5	56.6–200.6
50	34.8–227.5	47.8–188.7	67.5–148.2	71.6–141.4	75.6–135.4
100	35.3–221.1	48.9–182.0	70.7–139.6	75.8–132.0	81.1–124.6
500	35.8–216.2	49.9–176.7	73.9–132.3	80.3–123.3	88.3–113.2

estimates where taxa share common evolutionary histories, due to a problem of non-independence. A variety of 'clock' tests exist (e.g. see Sanderson 1997; Rambaut and Bromham 1998) although many lack power when applied to short molecular sequences. When rate variation is detected, lineages that are affected can be removed (linearized trees method, Hedges *et al.* 1996), the variation incorporated into a likelihood framework (Rambaut and Bromham 1998), or allowed to vary across the tree between constraining calibration points (Sanderson 1997; Huelsenbeck *et al.* 2000).

Molecular dating

Early molecular dating studies generally used a single gene, a few calibration points, and multiple pairwise distance comparisons between taxa to determine an evolutionary rate. Genetic distances between other taxa could then be converted to estimated dates of divergence, and were reported with confidence intervals associated with the estimation of genetic distance (or branch length), representing the phylogenetic component of variance (Fig. 5.3.6.1). More advanced studies increased the number of observed substitutions and rate estimates through the use of multiple genes and calibration points, respectively. The standard error around the mean of several estimates can be used as an estimate of experimental error, reflecting sensitivity to the data used (Hedges *et al.* 1996). Alternatively, quartets of taxa can be used to survey a large number of date estimates in order to detect variation, although problems of non-independence can again arise (Cooper and Fortey 1998). While such molecular dating studies have often included measures of phylogenetic and experimental error, few, with the exception of likelihood approaches, have specifically allowed for 'clock error'—errors due to the stochastic nature of the substitution process. Table 5.3.6.1 and Fig. 5.3.6.1 indicate the extent to which this oversight causes many published confidence intervals to be unrealistically narrow.

Using likelihood models

Likelihood techniques are attractive for molecular dating because the phylogenetic tree, calibration points, molecular sequences, and models of the substitution process can all be used as parameters in a likelihood model. The unknown divergence date and the evolutionary rate on its branch are the remaining parameters to be estimated. Such an approach can incorporate rate constancy tests and the estimation of confidence intervals as integral parts of the analysis, and can also allow for lineage-specific rate heterogeneity (Rambaut and Bromham 1998). To use the data in Table 5.3.6.1 (legend) as an example, a likelihood model can incorporate a fossil date for the divergence of the shearwater and loon to create a second calibration point and rate estimate, and the increased information results in a reduced 95% confidence interval of 81–139 Ma, an improvement of 17%. Because likelihood methods incorporate the variance associated with the estimation of phylogenetic, experimental, and substitution processes, it is illuminating to compare their more realistic confidence intervals with earlier molecular clock estimates.

Testing biological hypotheses

The uncertainty arising from the stochastic nature of the substitution process, and the imperfect estimation of

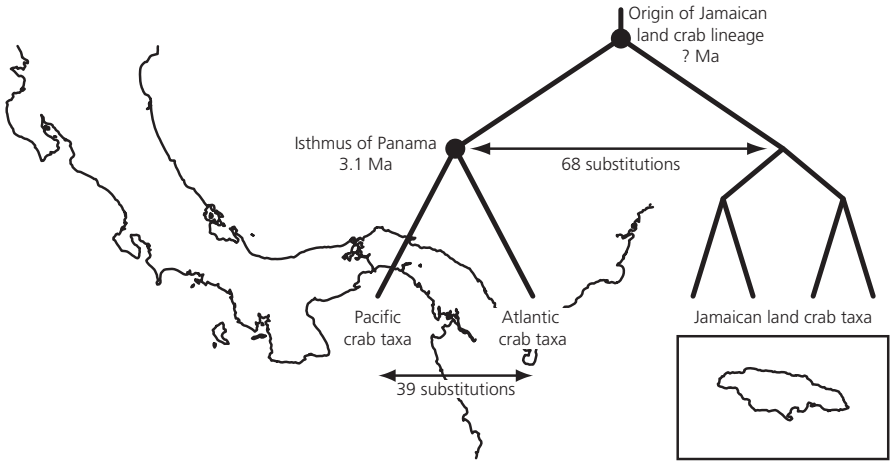

Fig. 5.3.6.1 Mitochondrial sequences from Jamaican land crabs have been used to suggest a recent terrestrial colonization (4.54 ±0.42 Ma), and accelerated rates of morphological evolution with respect to marine relatives (Schubart *et al*. 1998). The average genetic distance between marine crab taxa separated by the Isthmus of Panama (39 substitutions, ≈ 50), and the separation of marine and Jamaican land taxa (68 substitutions, ≈ 100) can be used (conservatively) with Table 5.3.6.1 to produce a 95% confidence interval of 3.25–6.42 Ma.

genetic distance and calibrated rates, limits the precision of molecular date estimates. However, date estimates with realistically large confidence intervals remain a useful addition to the palaeontological record, particularly when used to test specific hypotheses. For example, several studies have shown that molecular date estimates, even with relatively large confidence intervals, are still not compatible with the origin of metazoan phyla at the base of the Cambrian, or mammal and bird orders at the base of the Tertiary (Cooper and Fortey 1998; Rambaut and Bromham 1998). As improving technology makes longer molecular sequences more easily obtainable, the precision of molecular date estimates should increase considerably. Future developments using likelihood approaches, such as the incorporation of stratigraphic range statistics and multigene phylogenetic techniques, will further improve estimates. These improvements will ensure that the molecular record of past biological events becomes a worthy partner to the existing palaeontological record.

Consequently, even the variation associated with the substitution process produces a confidence interval 377% larger than the original branch length (phylogenetic) error estimate (±0.42 myr). The confidence interval would be wider still when other sources of error were included, such as different rates between island and marine taxa, and this limits the support for evolutionary hypotheses based on the molecular date.

References

Cooper, A. and Fortey, R.A. (1998) Evolutionary explosions and the phylogenetic fuse. *Trends in Ecology and Evolution* **13**, 151–156.

Hedges, S.B., Parker, P.H., Sibley, C.G. and Kumar, S. (1996) Continental breakup and the ordinal diversification of birds and mammals. *Nature* **381**, 226–229.

Huelsenbeck, J.P., Larget, B. and Swofford, D.L. (2000) A compound Poisson process for relaxing the molecular clock. *Genetics* **154**, 1879–1892.

Rambaut, A. and Bromham, L. (1998) Estimating divergence dates from molecular sequences. *Molecular Biology and Evolution* **15**, 442–448.

Sanderson, M.J. (1997) A non-parametric approach to estimating divergence times in the absence of rate constancy. *Molecular Biology and Evolution* **14**, 1218–1231.

Schubart, C.D., Diesel, R. and Hedges, S.B. (1998) Rapid evolution to terrestrial life in Jamaican crabs. *Nature* **393**, 363–365.

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5.4 Fossils in Stratigraphy

5.4.1 Stratigraphic Procedure

P.F. RAWSON

Introduction

Good stratigraphy still underpins successful research in all palaeontological disciplines, despite the development of theoretical approaches such as cladistics. It provides the ultimate time-framework against which theories and observations can be tested. Stratigraphy itself has evolved immensely since pioneers such as William Smith, Lyell, d'Orbigny, and Oppel developed the basic principles of stratigraphic procedure. But those basic principles are still fundamental: (1) to define and describe the individual rock units in the area of study (*lithostratigraphy*); (2) to correlate them with units elsewhere and with the standard time scale using all available means (e.g. *biostratigraphy, sequence stratigraphy, isotope stratigraphy*); and (3) to define (and refine) a standard global time scale (*chronostratigraphy*).

Stratigraphic codes and guides

Attempts to formalize procedures for classifying and naming stratigraphic units started at some of the early International Geological Congresses towards the end of the nineteenth century, and culminated in the publication of formal and informal guides, both international and national. The 'global' approach is represented by the work of the International Union of Geological Sciences' (IUGS) International Subcommission on Stratigraphic Classification (ISSC), which first published an exhaustive *International stratigraphic guide* in 1976 (Hedberg 1976) and has now issued a second edition (Salvador 1994). These owe much to earlier efforts by the American Commission on Stratigraphic Nomenclature and other national organizations, including the Geological Society of London.

The formal, rather 'legalistic' approach of the ISSC guide, coupled with differing approaches to stratigraphic practice in different countries, has led several national organizations to produce more informal guidelines. The second version of the Geological Society's *Guide to stratigraphical procedure* was aimed at the practising geologist, and opted for 'a degree of permissiveness' (Holland *et al.* 1978), especially in the accommodation of long-established stratigraphic names that did not follow current recommended procedure. The guide is now in its fourth version (Rawson *et al.* 2001) and, together with the ISSC guide, should be referred to for further information. In addition, the concepts and complex jargon of sequence stratigraphy are summarized clearly by Hallam (1992).

Lithostratigraphy

The establishment of a lithostratigraphic sequence that accurately reflects the physical characteristics and spatial relationships of all the rocks in a studied area is an essential prerequisite for further research. The basic lithostratigraphic hierarchy consists of:

Supergroup
Group
Formation
Member
Bed

This is now used globally. Lateral continuity (present or former) is an essential part of the definition of any rank of unit; hence most, though not all, lithological units tend to be limited to a particular sedimentary basin. The fundamental unit is the *formation*, generally defined as the smallest mappable unit. The formation should be lithologically distinct from adjacent units, but is not necessarily homogeneous. Formations may be partially or wholly divided into *members* to accommodate vertical or lateral lithological variation, such as a marginal sand. Individual *beds* are sometimes named, especially when they form important marker horizons, such as flint and marl bands in the Chalk Group. Two or more contiguous formations may form a *group*, which is defined either by its internal characteristics or (particularly in seismic and sequence stratigraphy) by the nature of its boundaries.

The *names* of units should embrace a place-name based wherever possible on the type section/borehole, a lithological descriptor if appropriate, and the rank (e.g. Speeton Clay Formation). In practice, old-established names that do not follow these criteria are often retained in a modified form, e.g. the Lias Group. The *boundaries* of units may be gradational or sharp, conformable or unconformable, isochronous or diachronous.

There is a separate terminology for igneous and metamorphic units, soil divisions, etc. (Salvador 1994; Rawson *et al.* 2001).

Correlation and relative dating

Biostratigraphy, the subdivision and correlation of sequences using fossils, is a fundamental tool in stratigraphy. The primary unit of biostratigraphy is the *biozone*, often more loosely called a zone. This concept originated in d'Orbigny's work but was developed in the 1850s by a brilliant young German worker, Albert Oppel, who divided the Jurassic of south-west Germany, France, and England into 33 zones, each named after a characteristic fossil, mainly ammonites. But from the beginning a zone was visualized as a bed or group of beds characterized by a particular fossil, rather than as an abstract time interval during which the fossil species actually lived. Thus a zonal name should only be used in the region where the index fossil(s) actually occurs.

Several types of biozone are recognized widely. They fall into three main groups: range, acme, and assemblage biozones (Fig. 5.4.1.1). Three types of range biozone are based on the total vertical range of an index taxon. A *total range biozone* is based on the total stratigraphic and geographical range of the index. A *consecutive range biozone* is based on the range of one species in an evolving lineage, and therefore can be the same as a total range biozone. A *local range biozone* is a more local version of the total range biozone, i.e. it reflects the total range in a localized area.

A *partial range biozone* is based on that part of the range of a taxon lying above that of one overlapping taxon and below that of another. Conversely, a *concurrent range biozone* is based on the overlapping range of two or more taxa. An *assemblage biozone* is more complex, reflecting overlapping and partial ranges of several taxa, one of which is chosen as the nominal index. Such zones are used mainly where fossils belonging to groups of poor biostratigraphic potential have to be utilized, as in the Lower Carboniferous limestones of south-west England. Finally, an *acme biozone* is based on a level of abundance of a taxon that has a greater overall stratigraphic range.

It is good practice for research workers to give a clear indication of which type of zone they are using (though even now only a small minority do so). It is also important to indicate the limitations in a zonation (such as those caused by gaps in distribution)—zonal tables often look suspiciously neat!

It has long been recognized that some fossil groups are better than others for correlation—simply because some evolved more rapidly and/or achieved a wider distribution than others. Thus trilobites and graptolites in the earlier Palaeozoic, ammonoids and conodonts in the later Palaeozoic, and ammonoids in the Mesozoic have provided prime tools for correlation. Biostratigraphy is a very practical aspect of palaeontology, however, and while it is often macrofossils that provide the 'ideal' zone fossil in terms of zonal duration, many practising biostratigraphers have to work on very small samples that yield microfossils alone. Thus microfossil zonations have been drawn up as an alternative to macrofossil zones. While the latter are normally defined by their base (the top being defined by the base of the next overlying zone), microfossil zones are often defined by the last occurrence (i.e. the first downhole appearance), to avoid the problem of contamination in boreholes.

Microfossil zones are generally longer-ranging, but geographically more widespread, than macrofossil zones. The need for a more refined correlation than is provided by zones alone has led micropalaeontologists and palynologists to highlight first and last occurrences (FO and LO) of individual taxa, and thus build up a detailed 'event' stratigraphy. For example, the LO of the nannofossil *Cruciellipsis cuvillieri* is currently used to define the base of the Upper Hauterivian (Lower Cretaceous) Substage (Mutterlose *et al. in* Rawson *et al.* 1996).

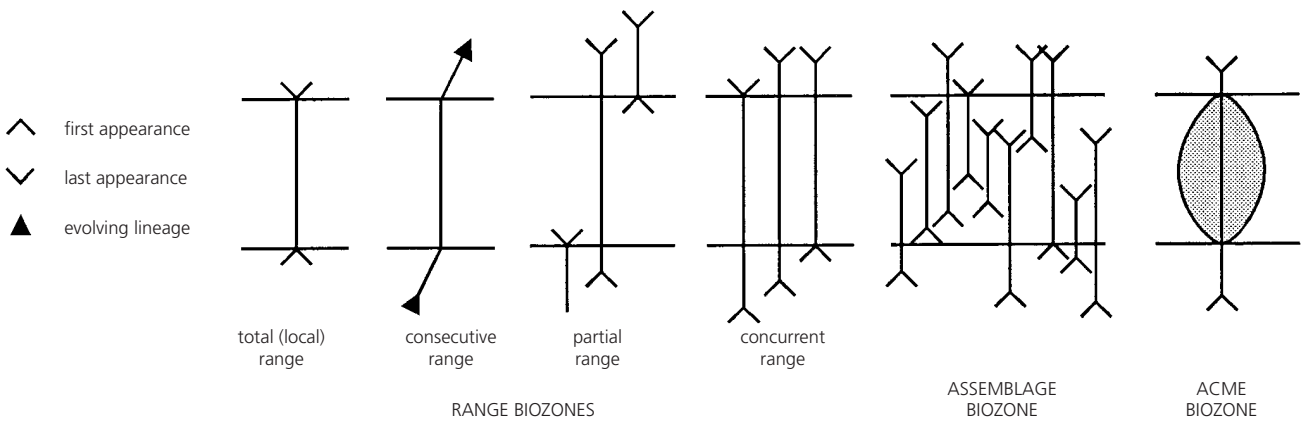

Fig. 5.4.1.1 Types of biozone.

For the Mesozoic, further refinement in macrofossil zonation has been provided by the developing recognition of ammonite biohorizons and zonules. Hence in the modern ammonite zonal schemes for the Jurassic a subbiozone may represent an interval of time of as little as 250 kyr, and a zonule less than 100 kyr. It should also be noted that many Jurassic ammonite workers regard their long-established ammonite zones and subzones as chronozones, the lowest subdivision of a stage.

While biostratigraphy still plays a fundamental role in the correlation of Phanerozoic rocks, other methods of correlation are becoming increasingly important and, particularly when integrated with the fossil evidence, can provide an ever-firmer basis for refining our relative time scale. *Graphic correlation* (Shaw 1964) is being used increasingly in the hydrocarbon industry. It brings together palaeontological and other data to produce lines of correlation (LOC) that can be used to date events and interpret depositional history.

One of the most widely applied, though contentious, methods of correlation derives from the application of *sequence stratigraphy* (see Section 5.4.5). This relies on interpreting rock successions across a basin in terms of sequences. A *sequence* is a package of strata bounded above and below by basin-wide unconformities or correlative conformities. Individual sequences can be very variable internally.

Sequence stratigraphy has become increasingly important in the three-dimensional analysis of individual sedimentary basins. Its application in broader correlations relies on the belief that individual sequence boundaries reflect rapid changes (rises or falls) in global sea level. Biostratigraphic evidence certainly suggests that *some* major breaks are more or less isochronous over large areas and thus of value in interregional or even global correlation. This has led to the construction of 'global' sea-level curves based on sequence stratigraphic analysis of basins from several continents. The best known and most widely used is the Exxon curve (Haq *et al.* 1987), though the global applicability of such a curve is still debatable and its uncritical use can prove very misleading (see Hallam 1992).

Sedimentary cyclicity at various scales is widespread in the stratigraphic record. The cycles that are of particular importance in correlation are those believed to have been caused by the *Milankovitch cycles* of precession (19 kyr and 23 kyr), obliquity (41 kyr), and eccentricity (100 kyr and 400 kyr). These astronomical cycles appear to have influenced sedimentation by causing cyclic changes in climate and oceanic productivity. The correlation of cycles from one section to another provides a powerful tool for correlation, especially when used in conjunction with biostratigraphy. The number of cycles in a particular sequence can also give a good numerical estimate of the length of time taken for the succession to accumulate—which can in turn test, for example, the duration of individual fossil zones (House 1985) or rates of evolution.

Rocks may preserve evidence of the nature of the Earth's magnetic field at the time they were formed. It is now clear that the field has reversed at irregular intervals, so that there have been alternating periods of normal and reversed polarity. Each change took place rapidly (over a few thousand years). The *polarity interval* (the period of stability between swings) varies from 100 kyr to several million years. The body of rock laid down during that interval forms a *magnetozone*. A relative magnetic time scale for the later part of Earth history (from the late Jurassic to the present) has been built up in great detail, and a less detailed scale extends back to the Palaeozoic.

Isotope stratigraphy is becoming increasingly valuable as an independent cross-check on global correlations made initially by other means. Isotopes of strontium, oxygen and carbon can all be fixed into the calcareous shells of marine organisms. The ratio of the two strontium isotopes ^{86}Sr and ^{87}Sr is constant throughout the oceans at any one time, but has varied slightly through time. Thus once a strontium isotope curve has been built up by using well-dated samples, other samples can be dated by comparison with the original curve.

Measuring $^{18}O:^{16}O$ isotope ratios is a well-established technique for determining palaeotemperature measurements. But fluctuations in $\delta^{18}O$ through time can also be used in correlation, mainly for the Cenozoic; working further down the column, it becomes increasingly difficult to produce a reliable $\delta^{18}O$ curve because of diagenetic problems. The carbon isotope $\delta^{13}C$ is less affected, and strong positive excursions in the isotope curve are often associated with black shale events. A comparison of both $\delta^{18}O$ and $\delta^{13}C$ curves for Upper Cretaceous rocks in Italy and England provides a good example of their potential, for it has pinpointed discrepancies in correlation at stage level as previously determined by biostratigraphic methods alone (Jenkyns *et al.* 1994).

Other methods of correlation that have proved immensely useful over considerable areas include the use of specific events, such as volcanic ash falls (*tephrostratigraphy*), or unique biological events, such as a sudden bloom of nannofossils. On a regional to local scale, the use of downhole tools in boreholes to measure the physical characteristics of the rocks drilled, such as natural radioactivity and electrical resistivity, provides *wireline log* correlations.

Holostratigraphy combines as many different approaches as possible to provide an integrated ('high resolution') correlation for the studied area or interval. It results in a much finer scale of correlation than can be obtained by any one method alone. Excellent results are

being obtained on, for example, the globally widespread Late Cretaceous chalks, which have proved difficult to correlate using biostratigraphy alone (e.g. Jenkyns *et al.* 1994).

The chronostratigraphic scale and the International Commission on Stratigraphy

Chronostratigraphy (time–rock stratigraphy) establishes age relationships based on rock sequences to build up a globally applicable standard time scale. This has been developed over the last 200 years (the current version appears on the endpapers of this volume). The main chronostratigraphic divisions are system, series, and stage (the corresponding time intervals are period, epoch, and age).

Although the time scale was initially a relative one, geologists have long tried to put numerical ages to it. The development of radiometric dating early in the twentieth century, and its continuing refinement to the present day, has provided a reliable method for numerical dating. In the process it has demonstrated the asymmetry of our time scale. Our nineteenth-century predecessors did not appreciate the immense length of 'Precambrian' time (some 4000 myr), over which only very broad divisions can be recognized. These are defined by numerical ages. Conversely, numerous divisions have been proposed for the relatively brief Phanerozoic interval (the last 540 myr), principally because the well-developed fossil record provided a fundamental means of division and correlation. Despite the subsequent development of many other methods of correlation, the asymmetry remains.

Many of the main divisions on the time scale are inadequately defined, so the main role of the International Commission on Stratigraphy (ICS), a constituent body of the IUGS, is to improve the scale by agreeing a definition for the basal boundary of each stage, series, and system. The upper boundary of each unit is defined by the base of the next overlying unit. Proposing boundaries is the responsibility of the various system subcommissions and working groups of ICS. The documented proposals are then voted upon by the voting members of ICS and, if approved, are published in *Episodes*. Completion of this procedure will eventually result in the whole of the Phanerozic sequence being divided into clearly defined time–rock units, the smallest of which (the stage) typically represents only a few million years of geological time.

In practice, boundaries are defined at a particular level in a body of rock at a specific locality, and not in abstract terms. The chosen locality and horizon are referred to as a *Global boundary Stratotype Section and Point* (GSSP). An imaginary 'golden spike' is placed at the GSSP, symbolizing that it should be valid for all time. (Some researchers would prefer an 'iron spike' which can rust away as knowledge improves!)

The importance of the 'golden spike' concept is that it marks an unique point in a rock succession that represents a specific point in time. How effectively a timeline can be traced from that point will depend on the accuracy of correlation achievable. The choice of a suitable GSSP is thus crucial. It must have the potential to serve as a 'global' standard for correlation. Selecting a suitable GSSP is difficult when so much research is still needed on many potentially important areas of the globe. Hence progress in the definition of GSSPs has been very slow, particularly for the Mesozoic and Cenozoic intervals. The GSSPs accepted up to the end of August 1999 are shown on the chronostratigraphic scale (see endpapers). While biostratigraphic criteria have played a fundamental role in their definitions, it is likely that some future GSSP proposals will depend primarily on other evidence. For example, it has been recommended provisionally that the base of the Aptian Stage (Lower Cretaceous) should be defined by a magnetic event rather than by an ammonite appearance (Erba *et al. in* Rawson *et al.* 1996), as the ammonite record at this level is still poorly known. This draft proposal has stimulated ammonite specialists to renew their research efforts.

The International Geological Correlation Programme

While the ICS's activities have promoted extensive research on correlation problems, the IUGS/UNESCO sponsored International Geological Correlation Programme (IGCP) has further strengthened international activity in this area. However, the aim of IGCP is much broader: to encourage and facilitate international cooperation in research on geological problems and thereby to promote the wise use of Earth as a human habitat and as the source of natural resources. Hence approved projects embrace a wide range of topics and disciplines. Recent programmes in which stratigraphy and palaeobiology play a vital role range from Project 335 (*Biotic Recovery from Mass Extinction Events*) through 345 (*Andean Lithospheric Evolution*) to 386 (*Response of the Ocean/Atmosphere System to Past Global Changes*).

References

Hallam, A. (1992) *Phanerozoic sea-level changes*. Columbia University Press, New York.

Haq, B.U., Hardenbol, J. and Vail, P. (1987) Chronology of fluctuating sea levels since the Triassic. *Science* **235**, 1156–1166.

Hedberg, H.D., ed. (1976) *International stratigraphic guide*. Wiley Interscience, New York.

Holland, C.H., Audley-Charles, M.G., Bassett, M.G. *et al.* (1978) A guide to stratigraphical procedure. *Geological Society of London Special Report* **11**.

House, M.R. (1985) A new approach to an absolute timescale from measurements of orbital cycles and sedimentary microrhythms. *Nature* **315**, 721–725.

Jenkyns, H.C., Gale, A.S. and Corfield, R.M. (1994) Carbon- and oxygen-isotope stratigraphy of the English Chalk and Italian Scaglia and its palaeoclimatic significance. *Geological Magazine* **131**, 1–34.

Rawson, P.F., Dhondt, A.V., Hancock, J.M. and Kennedy, W.J., eds. (1996) Proceedings 'Second International Symposium on Cretaceous Stage Boundaries' Brussels, 8–16 September 1995. *Bulletin de l'Institut Royal Des Sciences Naturelles de Belgique* **66** (Suppl.)

Rawson, P.F., Allen, P.M., Cope, J.C.W. *et al.* (2001) A guide to stratigraphical procedure. *Geological Society of London Special Report* (in press).

Salvador, A., ed. (1994) *International stratigraphic guide: a guide to stratigraphic classification. Terminology and procedure*, 2nd edn. Geological Society of America and International Union of Geological Sciences.

Shaw, A.B. (1964) *Time in stratigraphy.* McGraw-Hill, New York.

5.4.2 Calibration of the Fossil Record

S.A. BOWRING and M.W. MARTIN

Introduction

High-precision geochronology has revolutionized our understanding of how time is distributed in the rock record. Although geologists and natural scientists have known since the early nineteenth century that stratigraphic and palaeontological records are incomplete, only recently have palaeontology and geochronology united to allow the examination of evolutionary tempo as preserved in the rock record. This approach can be best described as *quantitative biostratigraphy*.

The geological record clearly reveals a few dramatic 'events' in the diversification and elimination of life—the Cambrian 'explosion', and the end-Permian and end-Cretaceous mass extinctions are the best known—but important questions remain regarding the tempo of biological diversification in general. For example, have there been evolutionary pulses that correlate with epochal changes in chemistry and temperature of ocean–atmosphere coupling and global climate? Does the aggregation and dispersal of supercontinents correlate with changes in patterns of evolution? How long does ecological recovery take following a major extinction? What are the durations of mass extinctions? The integration of detailed palaeontological, geochronological, and geological studies will allow these questions to be evaluated for the first time.

Geological time scale and correlation

The geological time scale has two components: a *chronostratigraphic scale*, based on a sequence of biological events, is calibrated in terms of a *geochronometric scale*, based on radiometric ages. The base of the Cambrian, the end-Permian extinction, and the well-known K–T boundary are defined on the basis of fossils in individual sections, and it cannot be assumed that the first or last appearance of a fossil occurs at exactly the same time in different depositional settings. Geochronometric calibration of a relative, chronostratigraphic time scale is straightforward. Ideally, a volcanic rock occurs very close to the point in a stratigraphic section chosen as the global stratotype for the boundary between two geological intervals, and the volcanic rock contains a mineral, such as zircon or monazite, for which a precise crystallization age can be determined. Such ideal situations are uncommon, however, and so calibration requires the dating of rocks in sections other than the stratotype which are then correlated to the stratotype by means of biostratigraphy, chemostratigraphy, and magnetostratigraphy. The terminal Neoproterozoic–Cambrian boundary, for example, is defined as a point in rock in a section located in south-eastern Newfoundland, but no volcanic rocks are present at, or in close proximity to, the boundary. Consequently, the age of the boundary can be calibrated only through correlation with other sections that contain datable volcanic rocks.

Due to the incompleteness of the geological record, and the facies-controlled occurrence of many diagnostic fossils, global correlations are fraught with difficulties. However, detailed global correlations between sections are now possible using chemostratigraphy, which assumes that carbonate rocks record a global signal of the geochemistry of sea water at a given time. Thus, the variations in signatures of carbon, oxygen, and strontium isotopes with stratigraphic position can be used to correlate between sections. This is especially useful for late Neoproterozoic and earliest Cambrian rocks which contain a paucity of biostratigraphically useful fossils (Kaufman *et al.* 1997). For example, Newfoundland lacks the small shelly fossils and the well-defined carbon-isotopic records that occur elsewhere. Other sections in north-western Canada, north-eastern Siberia, and Namibia contain all three elements and support the widely held view that the base of the Cambrian coincides with a sharp negative shift in the carbon isotope signal of 4–6‰ (Kaufman *et al.* 1997).

Most time scales assign an age to a particular boundary by considering all the available geochronometric data. Published chronostratigraphic time scales (e.g. Harland *et al.* 1990) typically assign an absolute age to a biostratigraphic boundary that reflects the averaging of several, often imprecise age determinations and

estimates; in the Palaeozoic the uncertainty is several million years. Both the number of calibration studies and geochronological resolution have dramatically increased in the past 10 years and this, in turn, has stimulated new palaeontological research. The combination of geochronology with biostratigraphy and chemostratigraphy provides an unprecedented level of resolution. Volcanic rocks can now be dated at the 1 myr or better level in late Neoproterozoic–early Palaeozoic time, and at the 500 kyr level in younger rocks. When combined with chemostratigraphy, the distribution of time can be estimated at an even higher resolution.

Methods for determining absolute time

Calibration of the fossil record requires a large number of high-precision ages from volcanic ash beds interstratified with fossil-bearing rocks. Since time is not linearly distributed in the rock record, stratigraphic thickness cannot be simply converted to time. Although ash beds are not common, they are being recognized with increasing frequency by stratigraphers and palaeontologists. In an ideal situation, the dating of multiple, closely spaced ash beds can provide an independent check on the resolving power of the technique because they must follow stratigraphic order from oldest to youngest.

Two geochronological methods that have proved to be the most reliable and capable of producing uncertainties in ages of 1 myr or less are $^{40}Ar/^{39}Ar$ and U-Pb geochronology. Both techniques are based on analysing single minerals separated from volcanic rocks. Whole-rock methods, like Rb-Sr geochronology, are much more susceptible to isotopic resetting and disturbance caused by metamorphism and fluid–rock interaction. In $^{40}Ar/^{39}Ar$ geochronology, sanidine, plagioclase feldspar, and biotite are the most commonly dated minerals. The basis of the method is the decay of K to Ar with a half-life of 1.25 Ga. Excellent results have been obtained for volcanic rocks that are Mesozoic or younger. Minerals from older volcanic rocks are more likely to have been altered by diagenesis or metamorphism which can cause open system behaviour, such as loss of the daughter isotope (Ar gas), or addition of the parent (K). In such cases a measured date has no geological significance.

U-Pb zircon geochronology has an advantage over other chronometers in that it exploits two independent decay schemes in a single U-bearing mineral. U has two major isotopes, ^{235}U and ^{238}U, which decay to ^{207}Pb and ^{206}Pb, respectively. This method provides independent age information and a test for the degree to which each system remained closed following crystallization. If a closed system has been maintained, the two U-Pb dates ($^{238}U/^{206}Pb$ and $^{235}U/^{207}Pb$) and the Pb-Pb date ($^{207}Pb/^{206}Pb$) for a zircon analysis should be the same, within uncertainties, and are referred to as concordant. High-precision Isotope Dilution-Thermal Ionization Mass Spectrometry (IDTIMS) allows small amounts of zircon that contain as little as $10–25 \times 10^{-12}$ g of radiogenic Pb to be analysed.

The power and potential of precise geochronology

High-precision geochronology has revolutionized the study of geological history. It is now possible to explore the connections between the biological and geological records with precise temporal constraints. The explosive diversification of life that occurred at ≈540 Ma and its catastrophic extinction at 251 Ma are arguably the two most important events in the history of life. Understanding the detailed history of these two events and the relationships between plate tectonics, ocean and atmospheric chemistry, and evolution requires a high-resolution temporal record. This effort requires a concerted effort by many workers and the development of new techniques to extract geological, geochemical, and geochronological information from the rock record.

A large number of high-precision U-Pb ages are available for volcanic rocks interlayered with fossil-bearing rocks (Fig. 5.4.2.1). Detailed palaeontology and geochronology indicate that the Cambrian explosion was more protracted than originally considered, and is best thought of as an interval of time (550–520 Ma) in which the preserved fossils increase in complexity, abundance, and size. Of particular interest is the discovery that the Lower Cambrian contains most of Cambrian time, with the Middle and Upper Cambrian representing only about 10 myr each. The highly resolved trilobite biostratigraphy of this interval, coupled with its short duration, allows detailed correlation, perhaps rivalling that of Jurassic ammonites.

The mass extinction at the end of the Permian is the most profound in Earth history (see Section 2.4.4). Geochronological results in southern China have constrained the marine extinction to an interval of less than 1 myr (Bowring *et al.* 1998), suggesting a truly catastrophic event. However, this discovery also raises a number of important questions that must still be addressed by detailed quantitative biostratigraphy. Does the extinction occur at exactly the same time across the planet? Does the extinction coincide with a large negative shift in the carbon isotopic composition of sea water? Does the terrestrial extinction occur at exactly the same time as the marine? Does the extinction occur at exactly the same time as the eruption of the Siberian Traps? Answers to these questions will be necessary to better understand the nature of the extinction mechanism(s).

Quantitative biostratigraphy will also enable the tempo of the end-Permian extinction to be compared

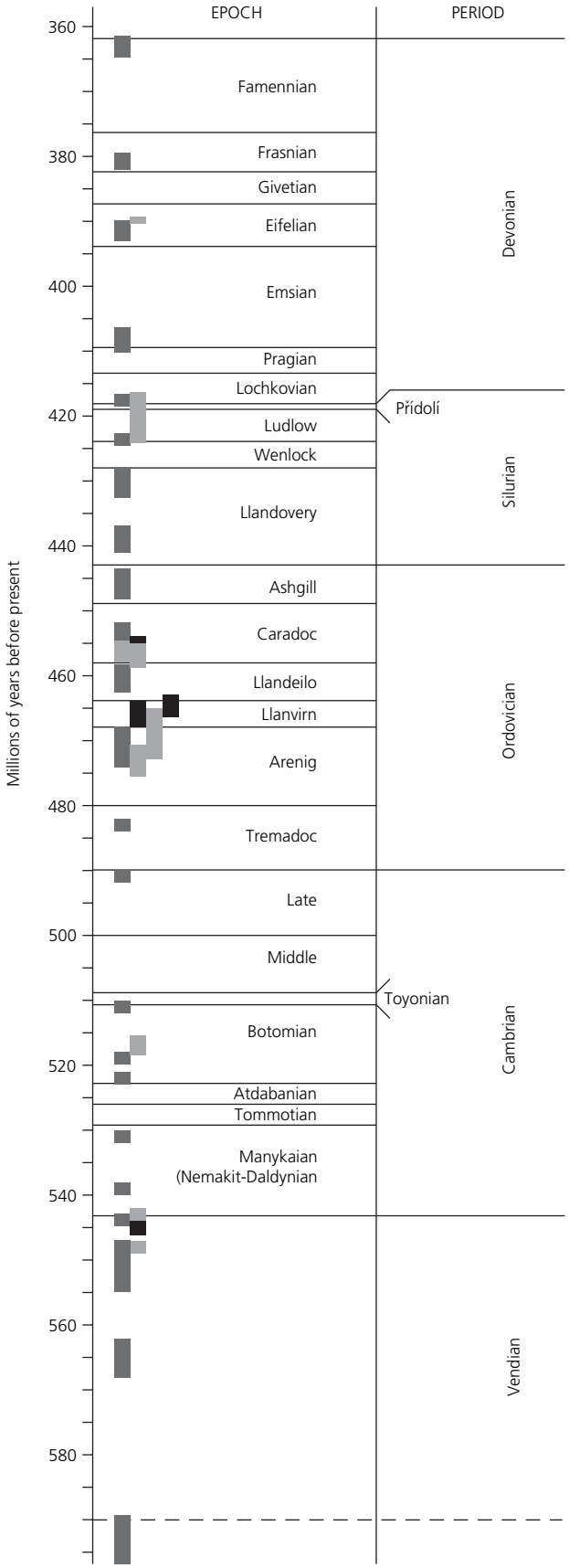

Fig. 5.4.2.1 Vendian to Devonian time scale based on available U-Pb zircon analyses (IDTIMS) dates from volcanic tuffs interstratified with biostratigraphically well-constrained sections. The length of each box displays two-sigma errors (95% confidence interval). Light and dark shading of boxes is to distinguish individual analyses. Data from Tucker and McKerrow (1995), Tucker *et al*. (1998), references cited by Bowring and Erwin (1998), and unpublished work.

with that of the other five or six major extinctions that punctuate the history of life. This comparison will allow the evaluation of whether most mass extinctions are driven by a common underlying cause, such as global anoxia or hypercapnia (CO_2 poisoning). In addition, a comparison of major radiatios and postextinction recoveries with the Cambrian explosion will help to identify what triggers rapid diversification in the record of animals. A detailed knowledge of how time is distributed in the rock record will lead to a much better understanding of the relationships between evolution and extrinsic environmental forces. When coupled with evolutionary biology, quantitative biostratigraphy will, for the first time, enable the influence of genetics and environmental forces on evolution to be compared.

References

Bowring, S.A. and Erwin, D.H. (1998) A new look at evolutionary rates in deep time: uniting paleontology and high-precision geochronology. *GSA Today* **8**, 1–7.

Bowring, S.A., Erwin, D.H., Jin, Y.G., Martin, M.W., Davidek, K. and Wang, W. (1998) U/Pb geochronology and tempo of the end-Permian mass extinction. *Science* **280**, 1039–1045.

Harland, W.B., Armstrong, R.L., Cox, A.V., Craig, L.E., Smith, A.G. and Smith, D.G. (1990) *A geologic time-scale 1989*. Cambridge University Press, Cambridge.

Kaufman, A.J., Knoll, A.H. and Narbonne, G.M. (1997) Isotopes, ice ages, and terminal Proterozoic earth history. *Proceedings of the National Academy of Sciences of the USA* **94**, 6600–6605.

Tucker, R.D. and McKerrow, W.S. (1995) Early Paleozoic geochronology: a review in light of new U-Pb zircon ages from Newfoundland and Britain. *Canadian Journal of Earth Sciences* **32**, 368–379.

Tucker, R.D., Bradley, D.C., Ver Straeten, C.A., Harris, A.G., Ebert, J.R. and McCutcheon, S.R. (1998) New U-Pb zircon ages and the duration and division of Devonian time. *Earth and Planetary Science Letters* **158**, 175–186.

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5.4.3 Confidence Limits in Stratigraphy

C.R. MARSHALL

Introduction

The fossil record is incomplete. Thus a literal reading of the fossil record will usually lead to inaccurate estimates of times of origin and extinction. However, quantitative methods are becoming available that can correct for this incompleteness of the fossil record (Paul 1982; see Marshall 1998 for a review).

Estimating the uncertainty in the position of the end-point of a stratigraphic range

Methods now exist for assessing the incompleteness of the fossil record in local sections. For example, assuming random fossilization, the average gap size in the observed range is an unbiased estimate of the distance between the last occurrence and the true end of the taxon's range (Fig. 5.4.3.1). Confidence intervals on the end-points of stratigraphic ranges are also easily calculated. The length of the confidence interval (r_c) for the true end-point of a stratigraphic range may be expressed as a fraction α of the observed stratigraphic range (R) (Strauss and Sadler 1989):

$$r_c = \alpha R \quad (1)$$

The value of α, assuming randomly distributed fossil horizons, depends on the number of fossil horizons within that range (H) and the confidence level (C):

$$\alpha = [(1 - C)^{-1/(H-1)} - 1] \quad (2)$$

The interpretation of the confidence interval is that the true end-point of the taxon lies within the distance r_c of the observed end-point with confidence C (Fig. 5.4.3.1). For many sections, however, the assumption of randomly distributed fossil horizons is manifestly violated, so the assumption must be tested in each instance.

Accommodating non-random fossilization

Two approaches for calculating confidence intervals that relax the assumption of randomly distributed fossils have been developed: (1) distribution-free confidence intervals; and (2) generalized confidence intervals.

The distribution-free method makes no assumptions about the distribution of gap sizes between fossils. By way of comparison, if fossilization is random, the gap sizes between adjacent fossil horizons will be distributed according to a very specific distribution, the Dirichlet distribution, which in turn leads to the simplicity of equation (2). The price paid for the relaxation of the assumption of random fossilization is that there are uncertainties associated with the sizes of the confidence intervals, and, unless the fossil record is unusually rich, it is not possible to place an upper bound on the size of the confidence interval for larger confidence levels. Despite the generality of the approach, it makes the restrictive assumption that there is no secular trend in gap size with stratigraphic position, an assumption not made by the generalized confidence intervals.

For generalized confidence intervals, a graph of the probability of recovering fossils as a function of stratigraphic position is required (Fig. 5.4.3.2), and R and r_c (equation 1) now denote the *areas* under the fossil recovery curve over the observed stratigraphic range and confidence interval, respectively. To apply the method, the distribution of fossil horizons must first be tested against the fossil recovery curve. Constructing fossil recovery potentials as a function of stratigraphic position is rarely easy and needs much work, but the method holds considerable promise.

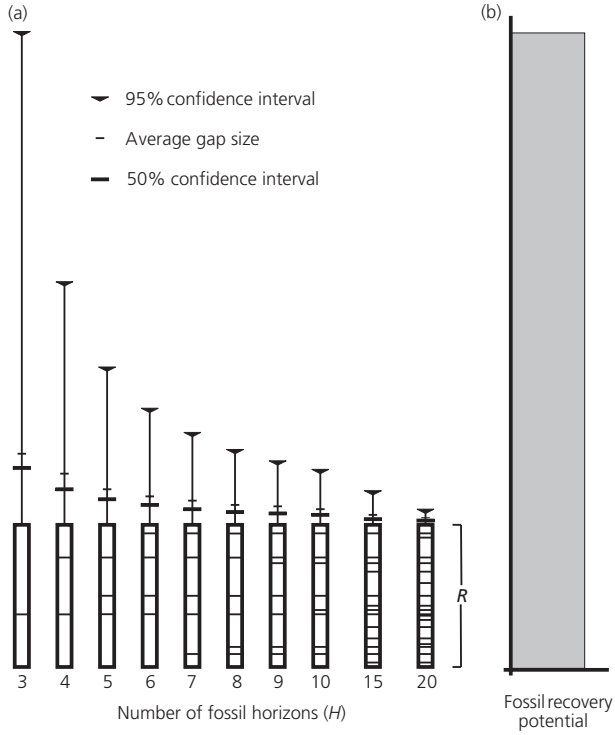

Fig. 5.4.3.1 (a) Sizes of the unbiased estimates (average gap size), and 95% and 50% confidence intervals on the true end-points of hypothetical stratigraphic ranges, calculated under the assumption that fossil horizons are distributed randomly (equations 1 and 2); bars within the stratigraphic range (R) represent fossiliferous horizons. (b) The assumption of random fossilization is equivalent to assuming a constant fossil recovery potential with stratigraphic position.

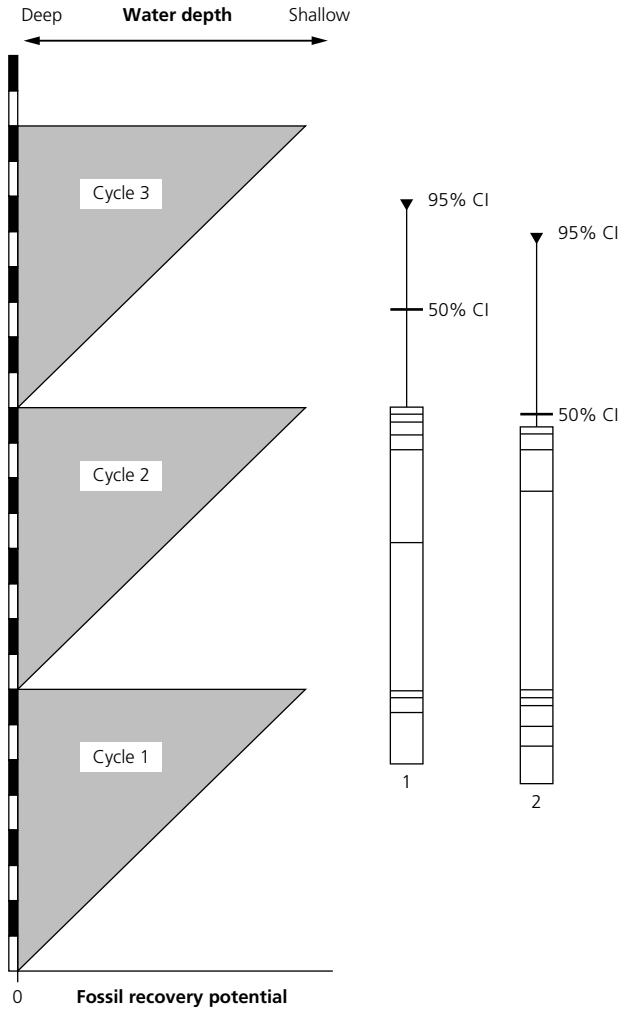

Fig. 5.4.3.2 Generalized confidence interval lengths take into account stratigraphically changing likelihoods of recovering fossils. Idealized fossil recovery potential for three shallowing-up parasequences for taxa with a preference for shallow-water facies is shown. Both species 1 and 2 have stratigraphic ranges of the same length, and are known from 10 fossil horizons, but the sizes of the generalized confidence intervals (especially the 50% interval) are of different lengths when the area under the fossil recovery curve is taken into account. (From Marshall 1997 with permission.)

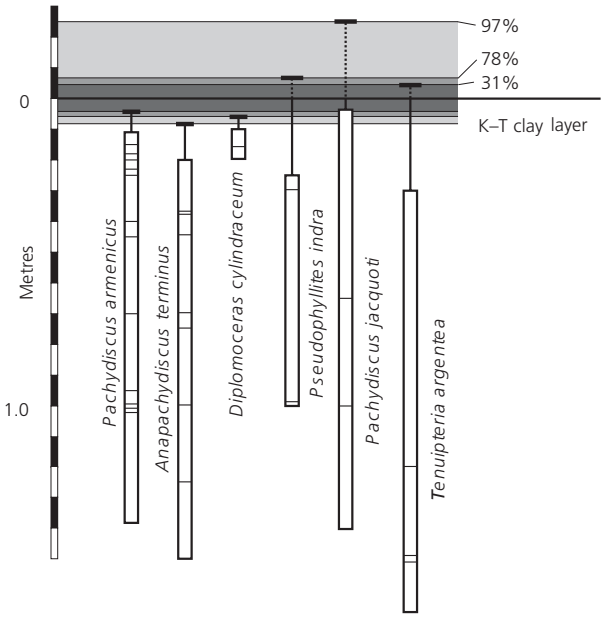

Fig. 5.4.3.3 Stratigraphic ranges of the inoceramid clam *Tenuipteria argentea* and ammonites known from two or more fossils in the last 1.5 m of the Cretaceous of the Bay of Biscay in Western Tethys. The 50% confidence intervals cluster around the iridium-bearing clay layer at the K–T boundary (indicated by the contours), suggesting that, despite their apparent gradual disappearance prior to the K–T boundary, they became extinct at the boundary. The exact position of the confidence interval end-points above the boundary are uncertain due to a change in lithology above the K–T boundary. The null hypothesis of randomly distributed fossil horizons (horizontal bars) could not be rejected for any species. (Modified from Marshall and Ward 1996.)

Distinguishing between sudden and gradual disappearances

Confidence intervals are particularly useful when analysing multiple taxa in local sections, especially for distinguishing gradual from sudden extinctions. With incomplete preservation, sudden disappearances of taxa will appear as smeared-out declines in diversity (the Signor–Lipps effect). Similarly, the first appearances of a set of taxa that all immigrated at the same time may also look smeared-out, giving the incorrect impression of sequential appearances (termed the Jaanusson effect by Marshall 1998). The '50% confidence interval' method may be used to distinguish between sudden and gradual extinctions (or originations). For a truncation event, the expectation is that half the 50% confidence interval end-points should lie above the truncation horizon, and half below (Fig. 5.4.3.3). A maximum likelihood approach for testing the null hypothesis of concurrent end-points has also been developed (reviewed by Marshall 1998).

Confidence intervals may be used to quickly assess more complex patterns of extinction or origination (Marshall and Ward 1996; Marshall 1998). First, the observed stratigraphic ranges, along with the 50%, 95%, and 99% confidence interval end-points, are graphed. To identify a catastrophic disappearance, the following rules of thumb are then applied: (1) putative truncation horizons occur in stratigraphic intervals bracketed by approximately equal numbers of 50% confidence intervals; (2) taxa that have last occurrences that lie stratigraphically higher than the interval identified by the 50% confidence intervals are excluded, on the grounds that they survived the truncation event; and (3) taxa with 95% or 99%

confidence intervals that lie below a stratigraphic interval identified as potentially including an extinction horizon are also excluded, on the grounds that they most likely disappeared before the time of the putative truncation event.

When applying this method it is important to remember that just because the null hypothesis of a sudden disappearance cannot be rejected for a set of taxa, this does not mean they disappeared catastrophically. Perhaps there was a relatively rapid but non-catastrophic disappearance that remains undetected due to the 'graininess' of the raw data. It is also important to remember that statistics are not concerned with questions of accuracy, but rather with questions of precision. The accuracy of the raw data must be established prior to analysis; all methods assume that fossils have been properly identified and that their stratigraphic positions were accurately recorded.

Interpreting disappearances

While these statistical methods may be used to test for different patterns in the fossil record, additional information is required to interpret the meaning of revealed patterns. For example, a variety of other explanations may account for an identified 'extinction' horizon: it may simply correspond to the top of the section, or to the upper limit of the collection effort; or it may be the result of taphonomic effects, or a facies change, or a hiatus in deposition, rather than a local or global extinction. To distinguish between these possibilities, information is required on the collecting regime employed, the sequence stratigraphic and facies architecture of the section (see Section 5.4.5), the taphonomic controls on the taxa of interest, and the global context of the section and its fauna.

When interpreting disappearances (and appearances) in the fossil record it is also important to remember that the extinction of a taxon name does not necessarily mean that the evolutionary lineage became extinct; it may persist under another name. Note also that where the extinction of a species is preceded by a dramatic drop in abundance, the fossil record is more likely to record the time of abundance drop (within the error bar of an appropriate confidence interval) than that of extinction. This may or may not be of concern. For example, if the question is whether a major geological or ecological event correlates with an observed change in the biota, it may be immaterial whether a species was decimated at that time, rather than becoming extinct. On the other hand, if the objective is trying to ascertain whether a lineage was simply extant some time after a major environmental change, then mistaking an abundance drop for an extinction could be a serious problem. The same note of caution holds for lineage appearances. If the time of origin is of interest (rather than the time when the species became ecologically important, for example), then the possibility of an extended period of cryptic existence makes the placing of error bars difficult.

Alternative sampling regimes

The methods discussed above assume that the exposure has been sampled completely and continuously, or nearly continuously. However, two alternative sampling regimes, binned and discrete, are commonly employed.

In binned sampling a section is divided into a series of contiguous bins, and at least the presence or absence of each taxon is recorded for each. In this situation a count of the number of bins containing fossils of a taxon will usually underestimate the number of fossil horizons (H in equation 2) that would have been observed with continuous sampling (so the confidence interval lengths will be overestimated).

With discrete sampling, small samples are usually taken at regular intervals and the taxonomic composition of each sample recorded. This is a standard way of sampling cores for microfossils. In discrete sampling most of the exposure, or core, is unsampled, and the estimate of the richness of the fossil record is much smaller than it would have been with denser sampling.

Equations (1) and (2) should only be applied to stratigraphic data derived from these types of sampling if it is felt that a decrease in the sampling bin size, or an increase in the discrete sampling density, would not affect the total number of samples yielding the taxon of interest. Methods for binned and discrete sampling regimes are currently being developed.

Global data

In standard global compilations, estimated durations may overestimate or underestimate true ranges, because true ranges are unlikely to coincide with the ends of the stratigraphic intervals of the first and last appearances. Assessing uncertainties in times of first and last appearance for global data is much more difficult than for local sections. Usually, quantitative data on the richness of the fossil occurrences that make up the ranges are not available and important sampling issues need to be addressed. For example, key stratigraphic intervals may not be represented by rocks over wide geographical areas, or those rocks, if they exist, may not have been searched adequately. The complexities involved in treating the incompleteness of the fossil record for global data still await full statistical analysis (but see Section 5.2.1). Crucial questions that need to be answered are: what level of precision does the question at hand require (maybe the incompleteness of the fossil record is not an issue); and what is the spatial distribu-

tion of the relevant rocks, and have they been sampled adequately?

References

Marshall, C.R. (1997) Confidence intervals on stratigraphic ranges with non-random distributions of fossil horizons. *Paleobiology* **23**, 165–173.

Marshall, C.R. (1998) Determining stratigraphic ranges. In: S.K. Donovan and C.R.C. Paul, eds. *The adequacy of the fossil record*, pp. 23–53. John Wiley, London.

Marshall, C.R. and Ward, P.D. (1996) Sudden and gradual molluscan extinctions in the latest Cretaceous in Western European Tethys. *Science* **274**, 1360–1363.

Paul, C.R.C. (1982) The adequacy of the fossil record. In: K.A. Joysey and A.E. Friday, eds. *Problems of phylogenetic reconstruction*, pp. 75–117. Systematics Association Special Volume no. 21. Academic Press, London and New York.

Strauss, D. and Sadler, P.M. (1989) Classical confidence intervals and Bayesian probability estimates for ends of local taxon ranges. *Mathematical Geology* **21**, 411–427.

5.4.4 High-resolution Biostratigraphy

J. BACKMAN

Introduction

Stratigraphy is concerned with the ordering and age relations of geological strata, and is therefore the basis for our understanding of Earth history from a chronological perspective. Biostratigraphy is the study of stratigraphy with palaeontological methods; the irreversible continuum of organic evolution as expressed in the fossil record is used to arrange rock units into relative order and to correlate them over geographical distance. There is no generally accepted definition of high-resolution biostratigraphy. It implies that fossiliferous samples are investigated at closer intervals in order to acquire more detailed information about their stratigraphic distribution. Here high-resolution biostratigraphy is illustrated by using the content of calcareous nannofossils in deep-sea sediments from the modern ocean basins. The key idea, however, can be applied to many, if not all, fossil groups from all parts of the stratigraphic column.

The term 'biostratigraphic resolution' is used to describe two different concepts. Firstly, it is commonly used to reflect rate of taxonomic evolution, e.g. the number of bio-events occurring per unit time. In this sense, the attainable resolution is limited by the fossil content of the rock record. Routine biostratigraphic work is rooted in the rigorous investigation of evolutionary emergence and extinction (first and last occurrences) of taxa in the rock record. Can biostratigraphic resolution be improved by using bio-events other than conventional appearances or extinctions? A class of biostratigraphic event that deserves much more attention is those that are based on various abundance relationships, such as consistent abundance crossover events (e.g. shift in dominance between ancestor and descendant species; Thierstein *et al.* 1977), or morphotypic outline or size changes (consistent shift in shape or size of species morphology that may be used for biostratigraphic purposes, e.g. Malmgren and Kennett 1982). The fossil record contains a huge reservoir of properties which are little explored and can be successfully employed in biostratigraphy.

Secondly, the term 'biostratigraphic resolution' is used to describe how precisely a specific bio-event can be resolved in terms of sample distance. In this sense, both geological and non-geological factors influence the resolution attainable, including productivity of the organism, sedimentation rate, thickness of the mean mixed layer (the mean depth of the layer immediately below the sediment surface that is homogeneously mixed by burrowing organisms), preservation state, sample intervals, sample preparation and data gathering methods. In deep-sea cores, the precision with which an event can be determined depends on the combined effect of sedimentation rate and depth of the mean mixed layer.

Investigation of sediment lightness and colour in a deep-sea core showed that significant information is preserved at the 1-cm scale in spite of bioturbation effects (Chapman and Shackleton 1998). In principle, there is no reason why useful biostratigraphic information could not be preserved at the 1-cm scale, even in settings other than deep-sea sediments. If the purpose is to maximize the biostratigraphic and palaeoecological information during the data gathering process, then high-resolution biostratigraphy must seek to use the smallest possible meaningful sample interval. A plethora of factors concerned with lithology, stratigraphy, and rates of sediment accumulation dictate that the smallest meaningful interval is on the centimetre level rather than the metre level.

The quantitative approach to gathering biostratigraphic data

Sampling strategy is of fundamental importance in palaeontological work. The Signor–Lipps effect, for example, is a much discussed example of how sampling bias may distort interpretations of biostratigraphic data; artificial patterns of extinctions may result from unevenly, or too widely, spaced samples (Glen 1994).

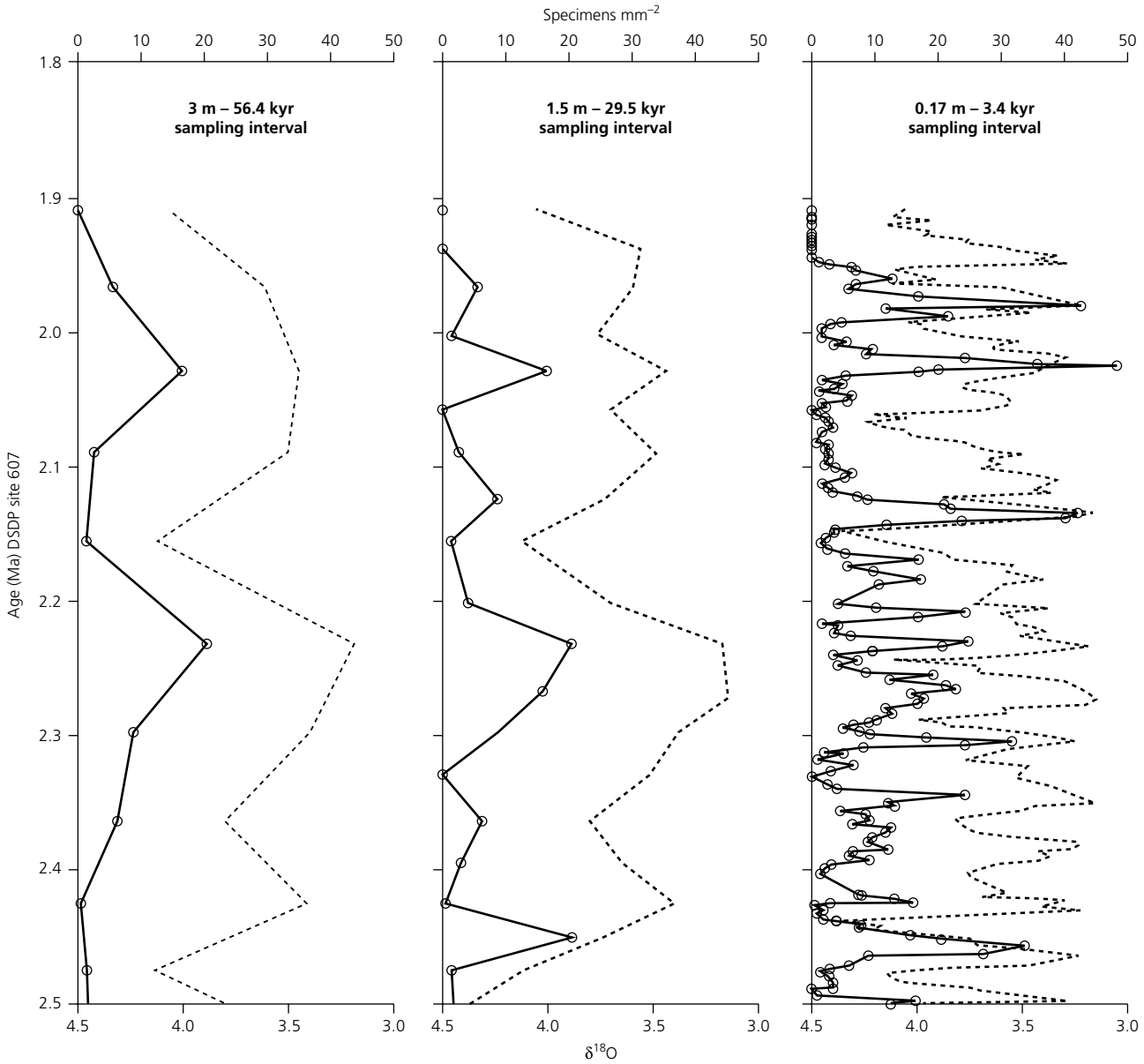

Fig. 5.4.4.1 Abundances of *Discoaster brouweri* (solid lines) and benthic oxygen isotope data (dotted lines; expressed in per mille relative to the PDB standard) from Deep Sea Drilling Project Site 607 in the mid-latitude North Atlantic Ocean. The fossil counts represent abundance per unit area on the smear-slide.

Experienced biostratigraphers commonly gather qualitative presence–absence data in a consistent manner. But gathering such data relies on a combination of judgements involving taxonomic identification and assessment of relative abundance (e.g. 'rare', 'common') that, in turn, depend on a series of other factors such as productivity, palaeoecology, and preservation. It is difficult for a non-specialist, sometimes even for a fellow specialist, to evaluate the meaning of 'common', i.e. to make an independent judgement of the nature of bio-events on the basis of qualitative presence–absence data. In contrast, a plot showing quantitative data can be readily assessed by most scientists.

A deep-sea record from the North Atlantic illustrates the importance of sampling strategy (Fig. 5.4.4.1). Using three different sampling intervals, abundance data from the final (Late Pliocene) part of the range of the calcareous nannofossil *Discoaster brouweri* are plotted together with oxygen isotope data. Variations in the benthic δ^{18}O record are dominated by the 41-kyr component of orbital

obliquity, representing the growth and decay of Late Pliocene ice sheets (Raymo *et al.* 1989).

The 3.0 m and 1.5 m sampling intervals, corresponding to approximately 56 and 29 kyr age spacing, do not capture the detailed record of environmental change that is preserved in the core. Furthermore, such coarse sample intervals do not reveal evidence of the dominant forcing mechanism of Late Pliocene climate change, as each obliquity cycle is represented by a single sample. Unfortunately the spacing of samples in deep-sea sediment records is typically of the order of 100–200 kyr because of lower sedimentation rates (≈1–2 m/100 kyr) than those exhibited by this example (DSDP Site 607; ≈5 m/100 kyr).

The abundance plots (Fig. 5.4.4.1) are based on census data. If the data plotted in the middle and left panels were expressed simply as 'few' or 'common', the utility of the dataset would further decrease. It would not yield any information about the palaeoecological response of the organisms to changing surface water conditions or provide a basis for assessments of the degree of sediment reworking. A major difference between the application of micropalaeontology and other analytical methods in palaeoceanography is that only the latter are routinely used at sampling intervals that are close enough to reveal details of palaeoenvironmental change. The success of modern palaeoceanography relies on continuous acquisition of quantitative data in a temporally, or stratigraphically, highly resolved framework. If this approach were adopted in marine micropalaeontology, it would certainly lead to a similar success.

The amplitude change in the abundance of *Discoaster brouweri* varies from about zero to about 20 units in the two panels showing coarser sampling intervals (Fig. 5.4.4.1), which represents only ≈50% of the actual amplitude. This emphasizes the need to analyse closely spaced samples in order to reveal the true variability of the fossil record.

The uncertainty of the position of the extinction event is determined to about 3 kyr (0.17 m) in the high-resolution study. The corresponding value for the 1.5 m sample interval is an order of magnitude less precise, and 20 times less precise for the 3 m interval. The abundance pattern of *Discoaster brouweri* varies with the isotope record; higher abundances occur during interglacials and vice versa. Not surprisingly, the spectral power density (a statistical method to determine if the dataset contains significant periodicity and, if so, at which period[s]) of the *Discoaster* record shows power concentrated almost exclusively at the 41-kyr period of obliquity (Chepstow-Lusty 1990), which highlights the fact that the variability of Late Pliocene surface water conditions (temperature, salinity, nutrient concentration) is preserved in the *Discoaster* record.

Chronological precision and synchrony

The high-resolution study (3.4 kyr sampling; Fig. 5.4.4.1) shows zero abundance in a series of samples above the final decline of *Discoaster brouweri* and throughout the following interglacial. The absence of this species throughout the interglacial provides substantial support for the extinction horizon at 1.95 Ma, with an uncertainty of a mere ±2 kyr. The development of astronomical time scales has paved the way for such precise biochronological estimates in Neogene and Pleistocene sedimentary records. This technique, which is based on orbital forcing, provides enormous potential for improving biochronology throughout the Phanerozoic. Rhythmical sedimentation is, after all, commonplace. Biostratigraphers must sample at close intervals in order to take advantage of the chronological resolution offered by the astrocycles as recorded in the sedimentary and fossil records.

Demonstrating the synchrony of biostratigraphic events in different deep-sea sediment records is a major problem, partly because of imperfections of the time scales used and partly through the variable quality of biostratigraphic data. Regardless of which part of the stratigraphic column is investigated, or whether shallow or deep-sea sediments are studied, sample spacings commonly represent chronological uncertainties of the order of ±500 kyr. Significant information about evolutionary processes, such as lineage splitting, is lost in such huge gaps of time, and migratory events appear as punctuated speciation or abrupt extinction. Recognizing the response of organisms to environmental changes at the Milankovitch band frequency simply requires adequate sampling strategies—at least a handful of samples per cycle.

Conclusion

Short sample intervals combined with quantitative data clearly represent a way to improve future high-resolution biostratigraphy, where the ideal datasets should represent the flux of species through time. Much remains to be done in all parts of the stratigraphic column.

References

Chapman, M.R. and Shackleton, N.J. (1998) What level of resolution is attainable in a deep-sea core? Results of a spectrophotometer study. *Paleoceanography* **13**, 311–315.

Chepstow-Lusty, A. (1990) *Nannoplankton as indicators of climatic variability in the upper Pliocene*. PhD Dissertation, Darwin College, University of Cambridge.

Glen, W., ed. (1994) *The mass-extinction debates: how science works in a crisis*. Stanford University Press, California.

Malmgren, B.A. and Kennett, J.P. (1982) The potential of

morphometrically based phylo-zonation: application of a late Cenozoic planktonic foraminiferal lineage. *Marine Micropaleontology* **7**, 285–296.

Raymo, M.E., Ruddiman, W.F., Backman, J., Clement, B.M. and Martinson, D.G. (1989) Late Pliocene variation in northern hemisphere ice sheets and North Atlantic deep circulation. *Paleoceanography* **4**, 413–446.

Thierstein, H.R., Geitzenauer, K.R., Molfino, B. and Shackleton, N.J. (1977) Global synchroneity of late Quaternary coccolith datum levels: validation by oxygen isotopes. *Geology* **5**, 400–404.

5.4.5 Sequence Stratigraphy and Fossils

S.M. HOLLAND

Introduction

Sequence stratigraphy is emerging as a powerful tool for understanding and predicting the structure of the stratigraphic record. Although originally developed for hydrocarbon exploration and later applied to basin analysis and facies models, sequence stratigraphy is being increasingly used to interpret the stratigraphic distribution of fossils. In addition, palaeontology is proving useful in aiding sequence stratigraphic interpretations.

The effects of sequence stratigraphy on the fossil record can be divided into those controlled by depositional environment and those controlled by sedimentation rate. Depositional environment strongly affects the taphonomy and palaeoecology of many organisms and causes taphofacies and biofacies to change predictably within depositional sequences. Other aspects of taphonomy and palaeoecology are controlled by sedimentation rates, which also change predictably within depositional sequences but often do not track facies. Because both depositional environment and sedimentation rate can change independently of one another, the expression of the fossil record varies dramatically within a sequence.

Although sequence stratigraphy has significantly increased our understanding of the stratigraphic record, it comes at the cost of an often-imposing terminology. To make matters worse, some authors have introduced redundant or unnecessary terms. In addition, misapplications of sequence stratigraphic principles abound. All of these problems can make an unassisted introduction to sequence stratigraphy difficult (see Van Wagoner *et al.* 1990 for a clear treatment of the principles of sequence stratigraphy).

Changes in facies within sequences

Sequences and parasequences are the two fundamental cyclic units of sequence stratigraphy. Sequences are built from parasequences, which are shallowing-upward sedimentary cycles bounded above and below by marine flooding surfaces. Facies within parasequences have gradational contacts and their transitions conform to Walther's Law, i.e. the vertical succession of facies corresponds to the lateral series of environments in which those facies were formed. Flooding surfaces are marked by the sharp juxtaposition of relatively deep-water facies on top of relatively shallow-water facies in a non-Waltherian relationship.

Groups of successive parasequences may show consistent internal changes in structure, such as progressive changes in water depth. Progradational parasequence sets are composed of parasequences in which each contains a shallower set of facies than the one beneath it, thereby forming a net shallowing-upward succession. Aggradational parasequence sets are composed of successive parasequences with no progressive change in facies composition and therefore no net trend in water depth. Retrogradational parasequence sets contain parasequences in which each contains a deeper set of facies than the one beneath it. Thus, retrogradational parasequence sets display a net deepening-upward trend, despite the shallowing seen within each component parasequence.

Parasequence sets are arrayed predictably within depositional sequences in what are called systems tracts, which are associations of all facies present at any moment in time (Fig. 5.4.5.1a). Type 1 depositional sequences consist from bottom to top of a lowstand systems tract that displays progradational then aggradational parasequence stacking, a transgressive systems tract with retrogradational stacking, and a highstand systems tract marked by initial aggradational stacking followed by progradational stacking. The flooding surface separating the lowstand and transgressive systems tract is called the transgressive surface. The flooding surface separating the transgressive and highstand systems tract is the maximum flooding surface and corresponds to the deepest water depths within a sequence. A type 1 sequence boundary marks the base of this entire succession and is identified by an abrupt basinward shift in onlap and facies. In downdip sections, this sequence boundary is characterized by a sharp contact at which shallow-water facies overlie deep-water facies. In updip areas, the basinward shift in facies is identified by a surface of subaerial exposure and erosion.

Type 2 sequences differ from type 1 sequences in that there is no basinward shift in facies accompanying the basinward shift in onlap at the underlying sequence

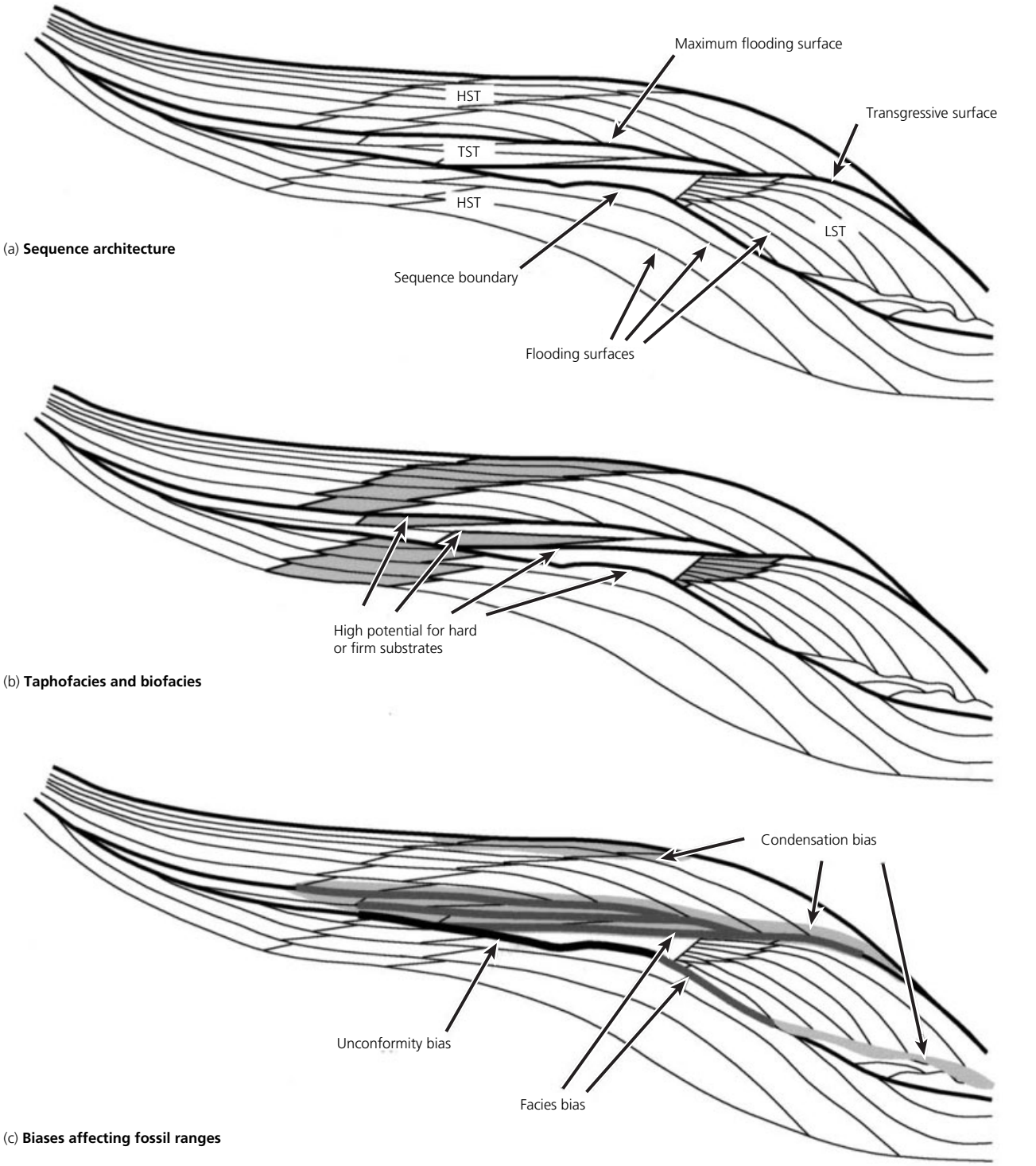

Fig. 5.4.5.1 Sequence architecture and its palaeontological effects. (a) Architecture of an idealized sequence; the three-dimensional shape of depositional sequences varies dramatically and can look markedly different from that shown here. LST, lowstand systems tract; TST, transgressive systems tract; HST, highstand systems tract. (b) Taphofacies and biofacies for a shallow marine environment. Note the large lateral shifts in the distribution of the biofacies at the sequence boundary and at flooding surfaces within the transgressive systems tract that give rise to faunal discontinuities. Note also that biofacies and taphofacies can recur within parasequences and sequences. Hard or firm substrates are likely to occur at the sequence boundary and at flooding surfaces within the transgressive systems tract and may give rise to unusual taphofacies and biofacies. (c) Biases that affect the range and first and last occurrences of species within sequences. The effects of sampling bias (not shown) can be felt throughout a sequence.

boundary. Although some subaerial exposure and erosion may occur landward of the highstand shoreline in a type 2 sequence, no change in facies or parasequence stacking occurs at the sequence boundary seaward of the shoreline. Consequently, type 2 sequence boundaries are essentially impossible to recognize within outcrops without the aid of seismic control. In addition, the shelf margin systems tract in a type 2 sequence replaces the lowstand systems tract of a type 1 sequence. Like the lowstand systems tract, the shelf margin systems tract is also characterized by progradational stacking that gives way to aggradational parasequence stacking. The two systems tracts differ in that the updip termination of the shelf margin systems tract does not lie below the shelf break of the underlying highstand systems tract, whereas the updip termination of the lowstand systems tract does lie below this shelf break.

Changes in sedimentation rate within sequences

In addition to facies composition, sedimentation rate varies markedly within sequences. Stratigraphic condensation, where timelines converge because of low rates of sediment accumulation, may occur anywhere in a sequence.

The flooding surfaces bounding every parasequence are surfaces of non-deposition and may also be subjected to minor submarine erosion. The degree of sediment starvation at flooding surfaces is much greater where facies changes are more pronounced, such as flooding surfaces within the transgressive systems tract.

Timelines converge and condensation results within sequences wherever there is onlap, downlap, apparent truncation, or toplap (Kidwell 1991a). Onlap is the termination of relatively flat-lying strata against an underlying sloping stratal surface. Downlap is the termination of dipping strata against an underlying relatively flat-lying stratal surface. Apparent truncation and toplap indicate termination of dipping surfaces against an overlying relatively flat-lying stratal surface. Toplap and downlap occur at the maximum flooding surface, onlap occurs at the sequence boundary, and toplap is most common near the top of the highstand systems tract (Fig. 5.4.5.1a). In each of these regions, sedimentation rates may be depressed and features reflecting stratigraphic condensation may develop. Although the maximum flooding surface is the most commonly cited zone of condensation, and is often referred to as the condensed section, maximum condensation commonly occurs elsewhere within a sequence.

Applications to taphonomy and palaeoecology

Ecological and taphonomic processes are so strongly controlled by depositional environment and by rates of sediment accumulation that both biofacies and taphofacies bear a strong connection to sequence architecture (Brett 1995, 1998).

Taphofacies

Taphofacies are most strongly influenced by water turbulence, availability of oxygen, and sedimentation rate. In many basins, turbulence and oxygen availability are closely tied to sedimentary environment, and as a result taphofacies are predictably arrayed within parasequences and sequences. Taphofacies influenced by turbulence and oxygen display the same shallowing-upward successions within parasequences, vertical trends within parasequence sets, and abrupt basinward shifts at sequence boundaries as occur in lithofacies.

Taphofacies influenced by sedimentation rate also occur in predictable settings within sequences. Low sedimentation rate taphofacies are common at flooding surfaces, as well as in zones of condensation such as around the maximum flooding surface, high in the highstand systems tract, and where there is onlap. High sedimentation rate taphofacies are found where progradation is rapid, such as in the dipping strata or clinoforms of the early lowstand and late highstand.

Of the many types of fossil concentrations, hiatal or condensed concentrations show perhaps the strongest relationship to sequence architecture and may form significantly thick shell beds (Kidwell 1991b). Such shell beds are commonly developed in zones of more significant stratigraphic condensation, such as regions of toplap, downlap, onlap, and apparent truncation. The taphonomic and palaeoecological attributes of these various major beds differ with their stratigraphic position (Kidwell 1991a). The formation of these major shell beds is further enhanced by taphonomic feedback, in which the accumulation of shell material favours colonization by additional shell producers, which may in turn add significant amounts of shell material.

Thin hiatal shell beds may form in zones of moderate condensation, such as at flooding surfaces. Lag concentrations of shells tend to form in shallow water environments and are expected to display facies tracking. Other shell beds may form through storm or event processes and are also expected to track particular facies, such as the lower shoreface.

Biofacies

Many biofacies show a strong relationship to water

depth, largely because those factors that most strongly affect the physiology and ecology of marine organisms (e.g. temperature, salinity, oxygen, light, nutrients, turbulence) are strongly correlated with depth. This tight relationship between biofacies and water depth explains why faunal tracking is a widely recognized pattern in which a given suite of species may recur multiple times within an outcrop as a given facies is repeated in successive parasequences and sequences.

Like lithofacies and taphofacies, biofacies display gradual vertical transitions where lithofacies change according to Walther's Law, such as within parasequences (Brett 1995). Where lithofacies change abruptly and do not conform to Walther's Law, such as at flooding surfaces and sequence boundaries, biofacies also change abruptly (Fig. 5.4.5.1b). These horizons of abrupt changes, or faunal discontinuities (Armentrout 1991), can be correlated, although the particular facies that immediately overlie or underlie these surfaces will change regionally. Faunal discontinuities are most prominent at major flooding surfaces, such as those within the transgressive systems tracts. Biofacies may also show abrupt changes at sequence boundaries as a result of prolonged non-deposition and erosion, as well as abrupt basinward shifts in facies.

Although soft-bottom biofacies are expected to dominate most depositional sequences and parasequences, firm-substrate and hard-substrate biofacies can develop in predictable parts of parasequences and sequences (Fig. 5.4.5.1b). Condensation at flooding surfaces, coupled with minor submarine erosion, favours the exhumation of semiconsolidated muds and the development of firmground conditions. Firmgrounds are more likely to develop at major flooding surfaces, such as those within the transgressive systems tract. Partial cementation and submarine erosion during periods of non-deposition may create a pavement of concretions on the sea floor, which can be encrusted and bored by a hard-substrate fauna. In carbonate settings, submarine cementation is commonly more extensive, leading to the formation of a hardground. Hardgrounds can record complicated histories of cementation, erosion, mineralization, and encrustation. Taphonomic feedback in these zones of low sedimentation can further aid the establishment of hard-substrate biofacies.

Applications to fossil ranges

Outcrop and modelling studies have shown that sequence architecture exerts a powerful influence on fossil occurrences and ranges (Holland 1995; Holland and Patzkowsky 1998). Palaeontologists have long recognized that times of first and last occurrence generally do not coincide with times of origination and extinction. This offset, known as the Signor–Lipps effect, is most widely understood as the reason why even catastrophic events, such as mass extinctions, may appear gradual in the fossil record.

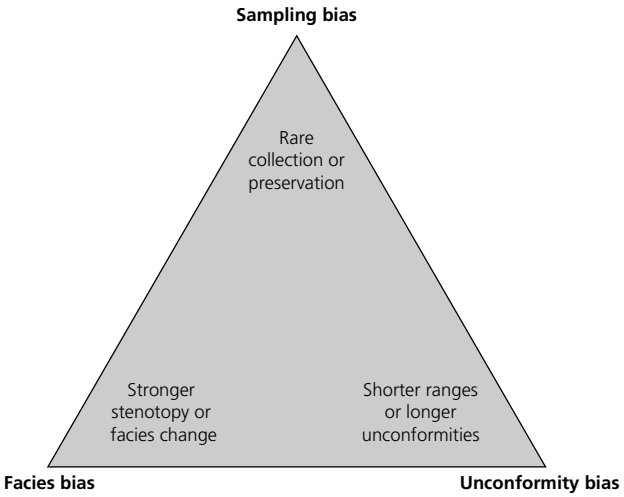

Fig. 5.4.5.2 Three components of the Signor–Lipps effect. Facies bias and unconformity bias are strongly influenced by sequence architecture.

Modelling reveals that the Signor–Lipps effect is actually a combination of several distinct factors, including sampling bias, facies bias, and unconformity bias (Holland and Patzkowsky 1999) (Fig. 5.4.5.2). Sampling bias is the result of the rarity of species and the frequency and intensity of collection. Increased rarity and decreased frequency or intensity of sampling all favour larger values of offset between the time of first or last occurrence and the time of origination or extinction. Facies bias is the result of the failure to collect species because of their restriction to particular facies. The effects of facies bias increase with the range of depth-dependent lithofacies present in a parasequence or sequence and with increasing stenotopy or facies specificity of taxa. Unconformity bias is the result of the wholesale removal or absence of the stratigraphic record and the fossils it contains. Longer unconformities and shorter ranges of species increase the effect of unconformity bias.

As components of the Signor–Lipps effect, all three biases cause first occurrences to be delayed from the time of origination and last occurrences to precede the time of extinction. Each of these three, as well as condensation bias, can cause more specific modifications of the fossil record. Facies bias, unconformity bias, and condensation bias can produce clusters of first and last occurrences in stratigraphic sections (Fig. 5.4.5.1c). These clusters correspond to the positions of faunal discontinuities between biofacies. At sequence boundaries in updip settings, subaerial exposure and erosion can cause long periods of no sediment accumulation. As a result, first and last occurrences of many species that became extinct during the

time of the hiatus may coincide with the sequence boundary. If a significant change in facies occurs at the sequence boundary in addition to the hiatus, facies bias will increase the number of first and last occurrences at the sequence boundary.

In downdip positions, subaerial exposure and erosion may not characterize sequence boundaries, but instead an abrupt basinward shift in facies may do so. Here, facies bias alone can lead to a concentration of first and last occurrences at the sequence boundary. The last occurrences at the surface will be dominated by relatively deep-water species that became extinct before the return of deep-water facies and the first occurrences will be dominated by shallow-water species that originated long before the appearance of shallow-water facies.

At major flooding surfaces, such as within the transgressive systems tract, facies bias can concentrate large numbers of first and last occurrences of species. Condensation bias can further enhance these spikes of first and last occurrences by allowing more time to elapse during which species can originate or go extinct.

Prolonged condensation around the maximum flooding surface can cause the clusters of first and last occurrences at flooding surfaces of the transgressive systems tract to be more closely spaced, further accentuating the apparent clustering of first and last occurrences. Condensation bias in the late highstand can also cluster first and last occurrences. Because this late highstand clustering is subject to erosion during the lowstand, it has a low likelihood of preservation, and these last occurrences will become clustered at the overlying sequence boundary.

None of these clusters of first or last occurrences necessarily represents clusters of originations or extinctions. These clusters arise because these horizons represent the first or last time these species could be collected in any given section as a result of missing time at unconformities or the facies specificity of the species. Furthermore, neither does the clustering of first and last occurrences suggest a causal link between position within a sequence and rates of evolution and extinction. Even where rates of origination and extinction are constant within a sequence, these clusters will occur. Clusters of first and last occurrences that do not coincide with these sequence stratigraphic settings are likely to be biologically real origination, migration, or extinction events.

Sampling bias, facies bias, and unconformity bias can also cause shifts in range offset, or the time lag between the time of first or last occurrence and the time of origination or extinction. Preliminary modelling suggests that not only are first and last occurrences clustered at sequence boundaries and major flooding surfaces, but those first and last occurrences are also more likely to have larger values of range offset. First and last occurrences that do not occur at these surfaces are likely to have lower values of range offset, and may be biostratigraphically more reliable.

Finally, all of these biases can strongly affect completeness of the fossil record. Preliminary modelling suggests that the effects of facies bias on completeness can equal or exceed those of sampling bias. Furthermore, in updip positions such as the coastal plain and cratons, unconformity bias can exceed the combined effects of both facies and sampling bias. Given that much of the fossil record comes from cratonic basins and the updip portions of coastal plains, these results suggest that the incompleteness of the fossil record may be largely the result of the incompleteness of the stratigraphic record. Unlike sampling bias, the effects of condensation bias, facies bias, and unconformity bias are not evenly distributed through the stratigraphic record, and as a result fossil occurrences commonly cannot be treated as if they were random with respect to stratigraphic position.

Prospects and conclusions

Sequence stratigraphy offers both promise and warning to palaeontology. The promise lies in the use of palaeontological data, such as biofacies, taphofacies, and patterns of first and last occurrences, as tools for aiding sequence analysis. The warning lies in the fact that many aspects of the occurrence of fossils cannot be read as simply as previously interpreted. Many palaeontological patterns generated by sequence architecture can mimic patterns of real palaeoecological, palaeobiological, and biostratigraphic interest.

For example, progressive shallowing or deepening within a systems tract can generate consistent vertical replacements of one species by another among several outcrops. The similarity in the vertical successions of these species may give the illusion of biostratigraphic utility, when in reality the species are tracking habitats and their ranges are diachronous.

The disappearance of species and the appearance of new forms, which may even share ecological similarities, may suggest extinction, origination, or migration events. In reality, such a pattern can result simply from a combination of sequence boundary and transgressive surface. If true extinction, origination, or migration events coincide with these surfaces, they will be difficult to distinguish from stratigraphic artifacts.

Finally, a species may appear and disappear repeatedly within an outcrop, suggesting a pattern of iterative evolution. In actuality, the species may be tracking habitats that recur in successive sequences.

These problems are made more pernicious by the observation that faunal change is much more prevalent within a series of facies than lithological change. Species are commonly more sensitive indicators of environment than are facies. As a result, lithology may appear to be

unchanging, yet species may be tracking habitats. Thus, lack of lithological change does not indicate a lack of facies bias. Similarly, recent stratigraphic studies have underscored the cryptic expression of many sequence boundaries. As a result, lack of lithological change does not rule out the presence of significant unconformity bias.

Two approaches are available for avoiding the potential misinterpretation of the fossil record. The first is to coarsen the scale of study, and sample a broad range of environments for any interval of time. This strategy is best suited for the study of long-term trends, such as the increasing interaction between shelly organisms and their predators in the Mesozoic and Cenozoic, or the pace of the Ordovician radiation.

When such coarser resolution is not acceptable, the second approach to overcoming these biases is to establish a high-resolution correlation framework that is independent of fossils. Sequence stratigraphy, event correlation, and chemostratigraphy may be the most suitable means of correlation. Once such correlations are established, a high-resolution time–environment approach can be used in which all facies of interest can be tracked through time, regardless of whether or not they occur in any given outcrop. Such a framework requires many sections arrayed across a long span of depositional dip. Studying numerous closely spaced sections, or sections spread along depositional strike, does nothing to counteract these biases. The distortions of the fossil record that result from facies control and sequence architecture can be greatly reduced by adopting either of these approaches.

References

Armentrout, J.M. (1991) Paleontologic constraints on depositional modeling: examples of integration of biostratigraphy and seismic stratigraphy, Pliocene–Pleistocene, Gulf of Mexico. In: P. Weimer and M.H. Link, eds. *Seismic facies and sedimentary processes of submarine fans and turbidite systems*, pp. 137–170. Springer-Verlag, New York.

Brett, C.E. (1995) Sequence stratigraphy, biostratigraphy, and taphonomy in shallow marine environments. *Palaios* **10**, 597–616.

Brett, C.E. (1998) Sequence stratigraphy, paleoecology, and evolution: biotic clues and responses to sea-level fluctuations. *Palaios* **13**, 241–262.

Holland, S.M. (1995) The stratigraphic distribution of fossils. *Paleobiology* **21**, 92–109.

Holland, S.M. and Patzkowsky, M.E. (1998) Depositional sequences and the stratigraphic distribution of fossils: isolating the effects of condensation. In: *1998 AAPG Annual Convention Extended Abstracts*, Vol. 1, p. A307. American Association of Petroleum Geologists, Salt Lake City, Utah.

Holland, S.M. and Patzkowsky, M.E. (1999) Models for simulating the fossil record. *Geology* **27**, 491–494.

Kidwell, S.M. (1991a) Condensed deposits in siliciclastic sequences: expected and observed features. In: G. Einsele, W. Ricken and A. Seilacher, eds. *Cycles and events in stratigraphy*, pp. 682–695. Springer-Verlag, Berlin.

Kidwell, S.M. (1991b) The stratigraphy of shell concentrations. In: P.A. Allison and D.E.G. Briggs, eds. *Taphonomy: releasing the data locked in the fossil record*, pp. 211–290. Plenum Press, New York.

Van Wagoner, J.C., Mitchum, R.M., Campion, K.M. and Rahmanian, V.D. (1990) *Siliciclastic sequence stratigraphy in well logs, cores, and outcrops*. American Association of Petroleum Geologists, Methods in Exploration Series no. 7, Tulsa, Oklahoma.

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